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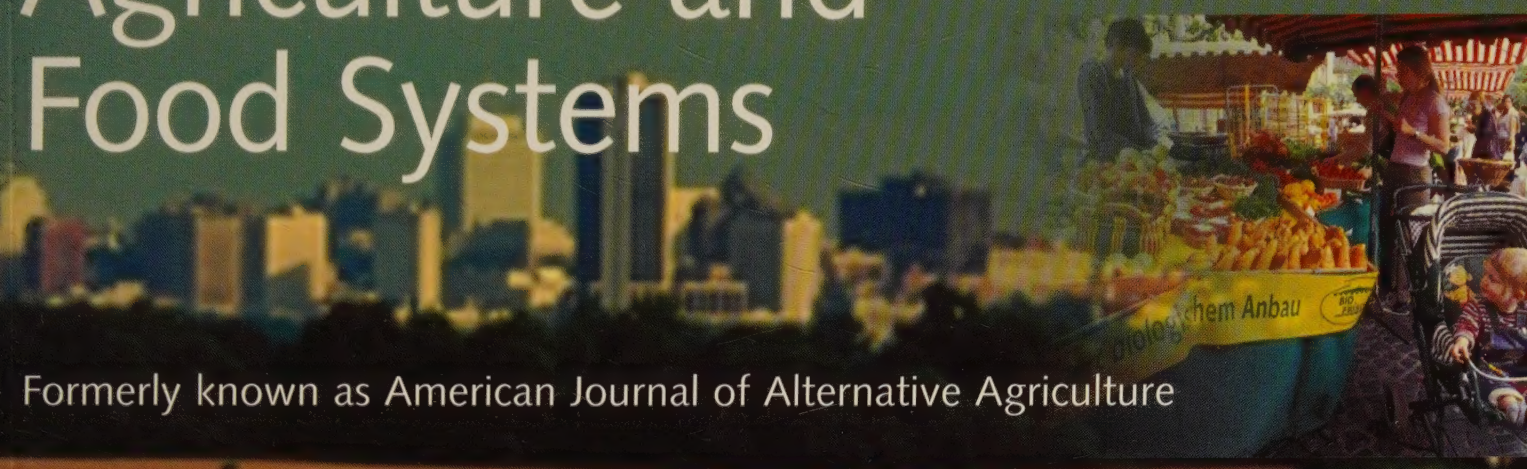

Formerly known as American Journal of Alternative Agriculture

Special Issue

Perennial Grain Crops: An Agricultural Revolution
Special Guest Editors:
Jerry D. Glover &
Wallace Wilhelm

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Renewable Agriculture and Food Systems

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Renewable Agriculture and Food Systems provides an international forum for original research and review articles on the biological, physical, social science, and policy aspects of alternative agriculture and food systems, focusing on the effective use of renewable resources and biodiversity in agro-ecosystems. The journal particularly welcomes multidisciplinary, holistic, systems research that addresses the multiple challenge of economically meeting basic human needs for food, fiber, and energy while maintaining essential natural and environmental resources.

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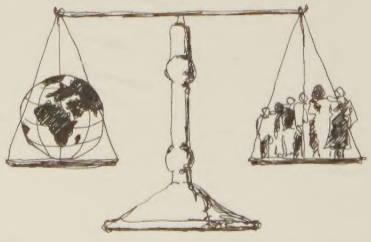

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The necessity and possibility of perennial grain production systems

Jerry D. Glover

Accepted 4 December 2004 **Forum**

A fundamental challenge of the 21st century will be to meet humanity's basic needs while maintaining soil, air and water quality and the integrity of remaining natural ecosystems. Chief among humanity's basic needs is food, most of which comes from highly managed croplands. More than two-thirds of global cropland features annual grain crops typically grown in monoculture. In contrast, the natural ecosystems displaced through agricultural conversion featured diverse perennial plant communities.

In nearly every instance, that dramatic conversion from perennial to annual plant communities impaired the very services—nutrient cycling, water management, soil conservation—essential for sustained agricultural production[1]. The resulting decrease in net primary production by annual croplands as compared to the displaced natural ecosystems[2] has been, in some regions, offset by unsustainable inputs of fossil fuels which further threaten the integrity of the planet's ecosystems[3].

The growing human population faces a seemingly intractable problem. Annual grain production, at its current scale, is fundamentally unsustainable, but humanity must be fed, and grain crops provide roughly 70% of humanity's food energy needs. A growing number of agricultural scientists seek a way out of this situation through development of perennial grain cropping systems. Managed with some level of diversity, perennial cropping systems promise many benefits in terms of land, water and wildlife conservation and decreased dependence on non-renewable energy sources[4]. In this issue, Crews[5], for example, outlines the greater ability of perennial plant communities, in general, to maintain, manage and cycle nutrients, and Cox et al.[6], highlight the ways in which diversity may be a critical tool in managing perennial production systems.

All recognize that high seed yields are a basic requirement for successful widespread adoption of perennial grain crops. The fact that no major grain crop is perennial is often used as evidence that perennials simply can't produce high yields of seeds. However, that all major grain crops are annuals may be more a result of their evolutionary history with humans than their oft-cited 'biology' as better seed bearers.

Domestication of annual grasses and legumes by early agriculturalists was fully integrated with annual food production practices. Seeds of wild annuals likely had many undesirable traits (e.g., shattering, non-uniform maturation) but improvements in desirable traits came rapidly as a natural result of annual harvesting of attractive seeds (e.g., non-shattered, large) and their subsequent annual resowing by humans[7].

Repeated harvests of edible seeds from perennial plants, on the other hand, would not require annual selection and replanting. Therefore, in the absence of a specific intention to breed perennial grains, perennial plants would have retained their undesirable traits. Very quickly, even semi-domesticated annuals would have been more enticing than their non-selected perennial counterparts.

Modern plant breeders, unlike those earliest plant breeders, have recent advances in plant breeding, unprecedented computational power and a greater understanding of ecology, cytogenetics and molecular biology to make high-yielding perennial grain crops possible. DeHaan et al.[8], in this issue, review the theory and strategy motivating current plant breeding efforts. They also indicate opportunities available to modern plant breeders to deal with the idea of a 'trade-off' between perennialism and seed production—the idea that there isn't enough plant carbon available to achieve both goals.

Satellite images of early-April plant activity in North America's Corn Belt graphically illustrate that 'trade-offs' in carbon allocation may actually favor perennials[9]. Most of the region is brown in early spring, indicating millions of square kilometers devoid of living plants despite adequate soil temperature, moisture and available nutrients. These extensive bare areas, seedbeds awaiting planting of annual crops, are maintained through heavy use of herbicides or tillage, and the loss of soil and nutrients offset through high inputs of fertilizers. Meanwhile, areas maintained under perennial vegetation show up as yellow and green, indicating the proper functioning of ecosystems whose deep, long-lived roots efficiently manage the available nutrients and water, build and conserve soil, and support the harvest of contemporary sunlight with no fossil fuel inputs and very little soil loss and water contamination.

Although satellite images of the region indicate little difference between photosynthetic activity of annual and perennial vegetation in mid-summer, the large areas devoid of living vegetation appear once more following harvest

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of the annual crops in the fall. In contrast, perennial vegetation continues to photosynthesize, drawing on resources from deep within the soil. These modern satellite images illustrate the history of agriculture and explain why agricultural conversion of natural ecosystems has nearly always cut into a landscape's productive capacity. For those working to develop perennial grain crops, the greater resource efficiency and productive potential of perennial plant communities shown by the satellite images offers great opportunity to meet humanity's food needs and maintain the planet's natural resource base.

Recent dramatic yield increases of annual grain crops, supported by high inputs of fossil fuels, provide opportunities and potential pitfalls. Today's high yields provide a relatively well-fed human population the opportunity to develop innovative, alternative farming systems for long-term survival and well being of the planet's inhabitants. The illusion, held by many, that these high yields by highly inefficient crop plants are sustainable, and not almost wholly reliant on an unsustainable infrastructure, is a serious pitfall. Affluent nations may afford that illusion for some time to come but many nations and the planet's ecosystems in general, in the face of increasingly scarce resources and degraded landscapes, can ill afford that illusion much longer.

Concerns over the time required to achieve high-yielding perennial grain crops are, for some, the larger issue. The next 50 years will be a period of rapid agricultural expansion, yet few advocating perennial grain crop development foresee significant commercial releases of perennial crops within the next 10 years, with a 25-year timeline being more realistic. While a 25-year timeline appears impractical in a world of 3-year research projects, the problems of soil erosion and degraded water quality resulting from annual cropping systems have been with us for millennia. If, in 25 growing seasons, there are productive agricultural systems in place that provide adequate yields, support vital ecosystem functions and are highly energy efficient, the time required for success will have seemed short.

Those working to develop perennial grain cropping systems do not advocate the immediate cessation of annual grain production, or eventual cessation of all annual grain production. Nor do they believe the development of perennial grain crops will solve all agricultural problems —there will be weed, disease, fertility, yield and management problems. These problems, however, will likely be less than in annual systems or, if worse for some problems, those problems will be offset by the overall advantages offered by the perennial systems. Such uncertainties must be weighed against the fact that we are at a critical juncture of necessity and possibility. The greater risk is not that we attempt and fail at developing perennial grain crops but that we do not try.

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Editorial response by Wallace Wilhelm: Some thoughts on perennial grains and polycultures

The paper by DeHaan et al. in this issue highlights advantages of perennial grain systems from the standpoint of environmental integrity and soil, water, and air quality. They discuss some of the complexity of developing a perennial grain crop, with emphasis on competition for photosynthate within the plant to produce both seed and perenniating organs. Cox et al. and Crews, also in this issue, extend the discussion of perennial grain systems and add the potential need to increase diversity to the system by using mixtures of cultivars or species to manage nutrient availability and diseases. These papers promote the concept of grain production systems that do not require annual planting, tillage, and substantial quantities of fertilizer and fossil-fuel-based chemicals to satisfy our

demand for low-cost, high-quality sources of dietary carbohydrate and fiber.

Although perennial systems are nature's model for environmental sustainability, these systems may not be without problems from a food and fiber production perspective. As Dr. Lee stresses in his short commentary (below), for identifiable reasons, humans have found annual grains to be more suited to providing the food and feed we need. In addition, the relatively short generation time and great diversity of traits in these annual species has allowed us to exploit annual grains to better provide food needs. Throughout the development of annual grains, cultural practices, uses, and marketing systems have evolved in concert. We currently have an elaborate system of production, marketing, and processing that is tuned toward annual, single-species grain crops. The current system, although dynamic, appears traditional, appropriate, and sustainable to many of those producing and processing the grain, as it does to most of the consumers of the products of the system.

Key problems that resist quick acceptance of a perennial grain are: (1) sinks competing for photosynthate within the perennial plant (seeds and perenniating organs); (2) if multiple species are needed for nutrient or disease management, as suggested by Crews and Cox et al., harvest and grain marketing systems incapable of coping with more than one species at a time; and (3) concern that the grain production capacity of the perennial systems will not have a yield potential to meet food and feed needs of the global population. These points and others are developed and explained in detail in a paper entitled 'Perils of production with perennial polycultures' by R.S. Loomis, slated for publication in the next issue of Renewable Agriculture and Food Systems.

The perennial grain system model nicely addresses some of the burning issues for agriculture and society: the need for maintaining the quality of our soil, water, and air resources; and our enormous dependence on the finite supply of fossil fuels and the aligned problems of greenhouse gas emissions and global warming. However, at present, the proposed systems fall gravely short in addressing another crucial issue, feeding the world population. Humankind has adapted and enhanced the productive potential of traditional (annual) grains for centuries and it may be unfair to demand equal production potential from the newly proposed perennial systems. However, for the concept to remain viable, proponents of perennial (and maybe polyculture) grain systems need to address these criticisms effectively and show substantial progress, both in theory and practice, toward production potential near that of the grains they espouse to replace. If the question of productive capacity is addressed adequately and small demonstrations of perennial grain systems show promise issues with market, traditional cultural practices, and processing will be overcome by the agricultural and food production and processing industry. The opportunity to provide food, feed, and fiber in a more sustainable manner is too great to overlook, but we must produce food and feed for today if we are to survive to meet and overcome the problems of tomorrow.

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Comments by Don Lee: Food, time and the prospects of annual versus perennial grain systems

The forum article by J.D. Glover ('The necessity and possibility of perennial grain production systems'), the series of articles authored by Glover's associates, and a preliminary review of cautionary comments by R.S. Loomis have motivated both my thinking and reflection. These varied viewpoints challenge us to think about environmental impact and cropping system productivity. These challenges are central to the thinking that my soil and plant scientist colleagues and I are paid to do in our professional lives. Weighing the scientific arguments of each viewpoint also caused me to reflect on the book *Plants, Man and Life* by Edgar Anderson (1952), assigned reading in my undergraduate plant taxonomy course, which I first read 20 years ago. An enduring take-home message Anderson delivered throughout his book was that the plants (crops, weeds and natives) we see are often growing where we find them, and have the traits they express, as a result of their evolutionary history with people.

People and biology both determine which grain-producing plants occupy our landscapes. Annual carbohydrate-rich grain crops grown in monoculture are the major systems people around the world use to obtain food and feed. Glover describes how these systems create environmental problems that the native perennial ecosystems avoid. Scientists recognize that the biology of annuals is focused by the need to produce seed for the next generation. Perennial plants can reproduce sexually, but they are biologically programmed to invest in themselves. Industry has certainly contributed to the scale and practice of annual monoculture production. However, *biology* is why successfully domesticated grain crops are annuals. People want seeds. Annuals specialize in seed

production and have been the people's choice for grain production.

Most people in today's world do not have the time or inclination to produce their own food. Consequently, grain yield continues as the driving force in determining what plants produce our food. Annuals provide production advantages, management choices compatible with mechanized agriculture, and the options for development and testing needed for our current economic and agricultural infrastructure. Under these food and time criteria, annuals continue to provide the *biologically superior* choice for grain seed size and quantity per unit area of land.

Glover prepares us for change as motivations increase for adding perennial grains to our cropping systems. Perennial crops could find a niche in the world's grain production systems if the right combination of: (1) environmental concern; (2) human time; and (3) improved grain yield potential emerge. Heightened environmental concerns and a greater availability of human time already exist to motivate the use of perennial grains in cropping systems in some parts of the world. Continuing work, such as that at the Land Institute, must lead to advances if we hope to increase grain yield and use of perennial crops. With time and combined efforts towards the right objectives, perennial grain crops could find a place in our food production systems. Ideally, providing adequate food to sustain both the people of the Earth and the soil, air and water resources on which we all depend.

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Perennial grain crops: A synthesis of ecology and plant breeding

L.R. DeHaan*, D.L. Van Tassel, and T.S. Cox

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Accepted 29 November 2004 **Review Article**

Abstract

Perennial grain crops would address many agricultural problems, including soil erosion, nutrient loss and pesticide contamination. Doubts about the possibility of perennial grain crops rest upon two assumptions: (1) that the relationship between yield and longevity is a fixed function that cannot be influenced by selection, mutation or environmental changes; and (2) that yield and longevity trade off in a bivariate manner to the exclusion of all other traits. These assumptions are consistent with the phenotypic trade-off model, but recent research suggests that a quantitative genetic model is a more appropriate approach to trade-offs. In the quantitative genetic model, environmental and genetic changes can result in increases in two traits simultaneously even when a trade-off, or negative correlation, exists between the two traits. Empirical evidence that the trade-off between perenniality and reproductive allocation is not fixed comes from wild, herbaceous perennials that can produce more than 2000 kg seed ha^{-1} in the temperate zone, and herbaceous perennial crops that produce on average 8900 kg fruit ha^{-1} in the tropics. Ecological literature suggests that most perennials produce small amounts of seed relative to their vegetative growth not as a physiological absolute, but rather as a result of natural selection in a stable, competitive environment favoring longevity. By selecting strongly for seed yield in a population of perennial plants, the plant breeder can likely achieve that which is rare in nature—a high seed-yielding perennial plant. The same general methodologies that have allowed annual grain breeders to increase grain yield and push many combinations of negatively correlated traits to levels of expression not seen in nature are available to the perennial grain breeder. Perennial grain breeders are integrating ecological principles and traditional plant breeding methods in their efforts to develop perennial grain wheat (*Triticum* spp.), sorghum (*Sorghum* spp.), sunflower (*Helianthus* spp.), Illinois bundleflower (*Desmanthus illinoensis*) and rice (*Oryza* spp.).

Key words: trade-off, carbon allocation, perenniality, life history, plant domestication

Introduction

Perennial grain crops would provide significant benefits to society and farmers[1]. New technologies and recent research make success more likely, but the task of breeding perennial grains remains formidable. Although strategies have been developed[2], plant breeders, working with other scientists, now need to establish and expand perennial grain breeding programs. The current structure of our public research institutions and a misunderstanding of the ecological and genetic principles that apply to perennial grain development impede that goal.

Specialization of scientific disciplines contributes to the problem. Ecologists and soil scientists have identified links between annual grain agriculture and environmental problems[3–7]. However, in formulating solutions involving plant breeding, they seldom look beyond a plant breeder's ability to increase the efficiency of existing systems[3]. Conversely, public plant breeders traditionally focus on the immediate needs of farmers, and allocate few resources to the longer-term project of breeding perennial grain crops. Privately funded or career-oriented plant geneticists are unlikely to invest in relatively long-term projects such as new crop development.

Attracting scientists to the field of perennial grain breeding requires articulation of the ecological and genetic principles central to the endeavor and securing funding sources sufficient to carry through the 25- to 50-year project required for developing a new crop. This paper provides a framework in which to consider these principles and describes their application in current efforts to breed several perennial grain crops.

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Alternative Approaches to Trade-off Theory

Supported by observations that wild annuals generally have greater reproductive allocation than wild perennials[8], some researchers conclude that perennial grain crops will be less productive than annual grains because of their greater allocation of assimilated carbon to storage organs[9]. Although we are unaware of any research that would rule out development of perennial grains, it is appropriate that we provide a theoretical foundation for their feasibility as we launch new breeding programs.

Much of the misunderstanding about trade-off theory has its roots in the phenotypic trade-off model. However, the phenotypic model—the older of two fundamental approaches to trade-off—has been shown to be inadequate, if not misleading[10,11]. In this model, the relationship between two traits is defined as a fixed function. Selection moves the main trait value along a curve defined by the function, but the function itself never changes. Only if trade-offs are held to be static and bivariate can the phenotypic model be applied to perennial grain breeding.

The alternative approach is the quantitative genetic model, in which the trade-off is described by a bivariate normal distribution[10]. In this approach, selection, drift and mutation can produce changes in the slope and intercept of the trade-off function. In this model, as in practical plant breeding, trade-offs are dynamic rather than static relationships, and multi-factorial rather than simply bivariate[10].

Photosynthate Production and Allocation

According to the phenotypic trade-off model, the exclusive use of annuals as grain crops was inevitable. Even if discussion is restricted to the allocation of a given amount of carbon for either seed or perennating structures, a gram-for-gram trade-off should exist only in the first year. After perennial roots and crowns are built, they need not be fully reconstructed in subsequent seasons (although portions die, regrow and respire). New buds which develop each year require energy, but energy is also present in the seed of annual plants. Much of the carbon allocated to perennation is not spent, because it is remobilized in the following season.

Perennials, starting the growing season with an extensive living root system, have the potential for greater photosynthate production than annuals. Perennial root systems better use water and nutrients in a greater volume of soil than annual roots not yet fully developed or that have already senesced[7]. Perennial sorghum (*Sorghum* spp.) plants in our Kansas nurseries emerge from large, starchy and cold-tolerant rhizomes 4 weeks before annual sorghum plants display their first leaves. Cool-season perennial grasses, such as intermediate wheatgrass (*Thinopyrum intermedium*) and perennial wheat (*Triticum* spp.)[12], also lengthen the growing season by tillering and photosynthesizing after harvest, through late summer and fall.

Plants can pay the energetic cost of perennation by harvesting a much larger fraction of the seasonally available photosynthetic energy. Furthermore, in an agricultural setting, the risk of poor establishment—frequently an issue with annual crops—is avoided in the years when perennials are regrowing. Stand thinning, which makes resowing necessary in perennial forages like alfalfa (*Medicago sativa*), may also limit the longevity of perennial grain crops. However, rhizomatous perennial forages can be very long lived[13], indicating that rhizomatous perennial grains may be a reasonable solution to the problem of stand thinning.

Ecologically, the costs of being a perennial are offset by the advantages. Globally, natural systems, primarily dominated by perennials, had greater mean net primary productivity than the anthropogenic systems that replaced them[14]. Within the USA Corn Belt, comparing near-wild perennials such as switchgrass (*Panicum virgatum*) to elite maize (*Zea mays*) cultivars in a high-input system may lead to the erroneous conclusion that perennials have inherently lower yields than do annuals. Comparing the productivity of domesticated crops within a family is more appropriate. For example, across diverse environments in the USA, the perennial forage crop alfalfa consistently produces more biomass than the annual soybean (*Glycine max*) (Table 1). The comparison is appropriate because both species are nitrogen-fixing legumes and the biomass of both species contains approximately the same level of crude protein[15,16]. Although at a disadvantage during its establishment year, alfalfa produces greater biomass yield than soybean, even when yields are averaged over the entire four-year lifespan of the alfalfa stand (Table 1).

If perennials can fix an adequate amount of carbon to make them viable crops, the question becomes one of harvest index rather than trade-off. The abundant seed yield of some wild herbaceous perennials lends support to the feasibility of perennial grain breeding. The perennial legume Illinois bundleflower (*Desmanthus illinoensis*) has had seed yields up to 1700 kg ha^{-1} in Kansas[17] and 3000 kg ha^{-1} in Florida[18]. *Senna marilandica*, another perennial legume, has had seed yields exceeding 2000 kg ha^{-1} [19]. These plants have yet to be used as grains, due to shattering and the need for extensive utilization research, not because of a yield trade-off. Further evidence comes from domesticated herbaceous perennials such as bananas (*Musa* spp.) and strawberries (*Fragaria* × *ananassa*) that, in Central America, 1999–2003, had an average annual reproductive allocation of 8900 and 2400 kg ha^{-1}, respectively[20]. The annual grains, maize (*Zea mays*), sorghum (*Sorghum bicolor*), rice (*Oryza sativa*) and wheat (*Triticum aestivum*), yielded an average of 2100, 2600, 3000 and 4200 kg ha^{-1}, respectively, in the same region and time period[20].

Table 1. Comparison of alfalfa and soybean biomass yields and standard deviations (SD) obtained in diverse environments.

Location	Alfalfa		Soybean[4]	
	Average	SD	Average	SD
	kg ha^{-1} yr^{-1}			
Urbana, Illinois, research station 2001–2003[1]	14,672		10,619	
Central Minnesota research station 2001–2003[2]	12,343		10,045	
Central Illinois on-farm production 1993–2003[3]	9,682	671	8,626	655
East-central Oklahoma on-farm production 1993–2003[3]	7,557	1,372	4,411	1,058
Northwest Minnesota on-farm production 1993–2003[3]	6,829	577	5,494	534
Average	10,216		7,839	

[1] Data from the University of Illinois Variety Testing Program, http://vt.cropsci.uiuc.edu/index.html. Alfalfa yields include an establishment year.
[2] Data from Minnesota Agricultural Experiment Station, http://www.maes.umn.edu/maespubs/vartrial/vt-cntnt.html. Alfalfa yields include an establishment year.
[3] Data from the United States Department of Agriculture National Agricultural Statistics Service, http://www.usda.gov/nass/
[4] Calculated based on a harvest index of 0.40.

Natural Versus Human-directed Selection

Most perennials produce small amounts of seed relative to their vegetative growth not because of inherent physiological constraints, but rather as a result of natural selection. The evolutionary concept that predicts higher average seed yield in annuals has been described as *r*-selection[21]. Wild annuals are typically found in less competitive (often disturbed), resource-rich, hazardous or changing environments. They typically evolve to use resources quickly and produce abundant seed that is widely dispersed and remains dormant until abundant resources are again available[22].

In a stable, undisturbed environment, competition results in resource limitation. Annuals are then mostly displaced by comparatively *K*-selected perennials, which have greater competitive ability and often dominate more resource-limited environments[21]. (To clarify, competition can result in resource limitation despite fertile soil and abundant rainfall.) To survive and reproduce in such a habitat, a perennial plant may develop a deep, spreading, long-lived root system. In order to shade its neighbors, a plant may grow tall and have horizontal leaves. Its leaves may contain more lignified tissues to increase leaf persistence[23]. In order to live in one place for many years, a plant must have robust mechanisms to fend off or tolerate herbivores and pathogens. Natural selection may have produced adaptations that allow the perennial plant to live through periods of extreme heat, drought or flooding.

Instead of producing seeds as its primary mode of dissemination, a perennial plant may instead invest in rhizomes that result in vegetative spread into favorable environments[24]. In response to stress, a perennial plant may shift allocation from seed production in a single season to rhizome production that increases the odds of survival[25]. Generally, low levels of dormancy in the seeds of perennials compared to annuals[26], combined with the scarcity of long-lived grass seeds found in seed banks[22], leads to the conclusion that seeds of perennials are used more for dispersal than for survival through time[27]. Seed production is only one of many traits important to the perennial plant's overall fitness under natural selection. If natural selection is not acting strongly for seed yield relative to the aggregate of many other traits in a perennial plant, low seed yield is expected. Indeed, there is evidence that fitness in perennial plants tends to depend more heavily upon survivorship than on fecundity[28].

Because *r*- and *K*-selection are comparative terms[21], their use in separating species into neat categories is a misapplication. Even wild plant species cannot be segregated in such a way, and with artificial selection in agricultural fields, a much wider range of trait combinations is possible. For example, annual types of wild rice (*Oryza* spp.) typically produce more seed than related perennial types, because of their long history of *r*-selection[29]. Annuals produce more seed in response to selection for a greater rate of population increase, while perennials 'show greater vegetative allocation which helps them maintain themselves in crowded habitats'[29]. Allocating a larger proportion of resources to seed and less to vegetation would be one avenue for obtaining a high-yielding perennial grain in an environment where less vegetative growth is needed.

Much of the yield gain in annual grains has come by reducing intra-specific competition, increasing tolerance to crowding stress, increasing responsiveness to high inputs, reducing height and/or increasing harvest index[30–32]. Modern grain plants have a narrow plant profile that reduces competitiveness, and they are often short, in order not to waste resources on vegetative biomass or lodge when nitrogen fertilizer is applied (Fig. 1). In contrast, most wild perennials are extremely competitive. Perennial grain plants should be selected to expend less energy on competition and more on seed production. The goal is a perennial grain crop with deep, durable roots with an above-ground structure that resembles that of annual grain crops more closely than it does that of wild prairie plants (Fig. 1).

Figure 1. Archetypal morphology of (a) wild annuals; (b) early annual grain crops; (c) modern annual grain crops; (d) wild perennials; and (e) future perennial grain crops.

Anticipated Difficulties

Because perenniality[33] and yield are both polygenic traits, we do not expect that a 'yield gene' can be inserted into a wild perennial, or a 'perenniality gene' into an annual crop plant. Rather, perennial grain breeders are pursuing two parallel strategies: domesticating promising wild perennials and hybridizing annual crops with perennial relatives. In either case, one of the major obstacles we face is the anticipated negative correlation (or trade-off, properly understood) between yield and longevity.

In most cases, multiple traits associated with fitness are expected to be negatively correlated. This is because alleles conferring a positive effect on multiple fitness traits have been largely fixed within a population, leaving those responsible for negative correlations at more intermediate frequencies[34]. Therefore, we fully expect seed yield and longevity to be negatively correlated in perennial grain populations. Selecting to increase seed yield and longevity simultaneously will be slower than selection for either yield or longevity alone. Plant breeders are familiar with the challenge of selecting against negative correlations, as when they attempt to improve concentrations of oil or protein in the seed[35,36] without reducing grain yield. Despite negative correlations, breeding has increased seed yield in perennial forage species[37], while simultaneously increasing forage yield[38]. (The typically small increases in forage and seed yield observed in perennial forages are due to unique challenges in the forage industry[39] that should not be generalized to the breeding of perennial grains.)

Hybridization between annual crops and wild perennials, with the goal of perennial grain development, is made more difficult by genetic and cytological divergence of the parents. Wide hybridization often produces highly sterile progeny. Restoring fertility can be a lengthy process, or even end in failure. Whether or not fertility is restored by chromosomes doubling, lack of pairing between chromosomes derived from different parents can mean that

linkages between genes conferring perenniality and genes that limit yield are difficult or impossible to break.

An Integrated Conceptual Framework

Even as we make the case that breeding perennial grain crops is a realistic objective, the relationship between perennial grain development and ecological trade-off theory remains unsettled. Plant breeding literature generally assumes a human-modified environment and artificial selection. Ecological literature has often focused on a single natural ecosystem, seldom considering the role of artificial selection. In an effort to explain perennial grain breeding in a manner that is equally satisfying to ecologists and plant breeders, we have developed a framework that integrates plant breeding and ecology through the quantitative genetic approach to trade-off theory.

The context of a stable environment, in which natural selection acts in a constant way, provides a useful starting point for discussion. Assuming no mutations, selection will eventually exhaust additive genetic variance for fitness, and fitness will no longer increase. At that point, the population is said to be at equilibrium. Falconer and Mackay state that:

> Since the array of gene frequencies in an equilibrium population is the best, in the circumstances, for maximizing fitness, it follows that if selection is applied to any metric character that is not fitness itself, the gene frequencies at loci affecting the character must change if there is a response. Fitness must therefore be reduced as a correlated response, unless the character selected is controlled entirely by genes with no effect on fitness.[34]

In other words, natural selection will, in a stable environment, result in the optimal allocation of resources. By definition, the highest value of any character that is not fitness itself will not result in the highest fitness.[34]

A brief note on the terms 'fitness' and 'stability' is appropriate at this point. In natural systems, fitness integrates virtually all plant traits. On an agricultural research station, the plant breeder selects certain individuals or families based on any character or combination of characters, thereby defining fitness. And, of course, no environment is truly stable. The adaptive landscape model of selection deals with this fact[40]. However, making the assumption of a stable environment allows easy conceptual consideration of the quantitative genetic principles involved in trade-off theory.

As Lack[41], the father of trade-off theory, was careful to state, a trade-off must hold only in a specific environment[41,42], and Falconer and Mackay[34] further stipulate that the concept of an equilibrium population includes the assumption that mutation does not occur. But environments fluctuate and mutations do occur, so trade-offs are never absolute.

The conceptual model depends upon an understanding of annuality and perenniality as quantitative traits that respond to selection in the same manner as more commonly considered quantitative traits, such as seed yield or seed protein content. Thomas et al.[43] have made a strong argument that although perennials and annuals may appear to be dramatically different, vastly different life histories can occur as the result of minor quantitative changes. They conclude that 'annuality and perenniality are traits that recur time and again across the taxonomic range and that, with the right selection pressure, the propensity to generate either form of phenotype can be realized without the need for large-scale genetic innovation'[43].

Domestication and the Breeding of Annual Grains

For greater clarification of a topic that spans several disciplines, our conceptual model can be used to examine how trade-off theory applies to wild and domestic forms of annual and perennial plants (Fig. 2). The model is not quantitative, and the steps in the model are not inevitabilities. Rather, the model is intended to provide a framework in which to consider what is possible and, perhaps, likely due to natural and artificial selection.

The model assumes that carbon allocation is completely partitioned among five types of organs and functions: (1) seeds, (2) storage organs, (3) defense structures and compounds, (4) leaves and stems, and (5) roots. The metric used is the average annual carbon irreversibly allocated for each function, averaged over the life of the plant. This allocation includes the carbon used for respiration in that organ or function, averaged over the life of the plant, but not carbon that is remobilized for a different function. Carbon allocation is assumed to represent allocation trade-offs accurately. Where equilibrium populations are considered, we also assume that environments are completely stable and that there is no mutation.

The starting population (Fig. 2a) is one of short-lived perennial plants (with 'short-lived' defined relative to other populations in the model) in an environment with moderate disturbance and resource availability. Through natural selection the population has achieved maximum fitness within the constraints of its genetic variation by allocating nearly equal amounts of carbon to roots, leaves and stems, defense and storage, and a small amount to seed. Therefore, it is considered to be in equilibrium.

Water, light and nutrients are more abundant in an agricultural field than in the starting environment (Fig. 2b), due to regular disturbance and a variety of inputs. If a short-lived perennial population invades the field and is able to avoid cultivation during the growing season, the greater resource availability will cause an increase in growth in all structures except roots, which typically do not grow as large relative to above-ground biomass in nutrient-rich environments[44,45]. Because natural selection has not yet

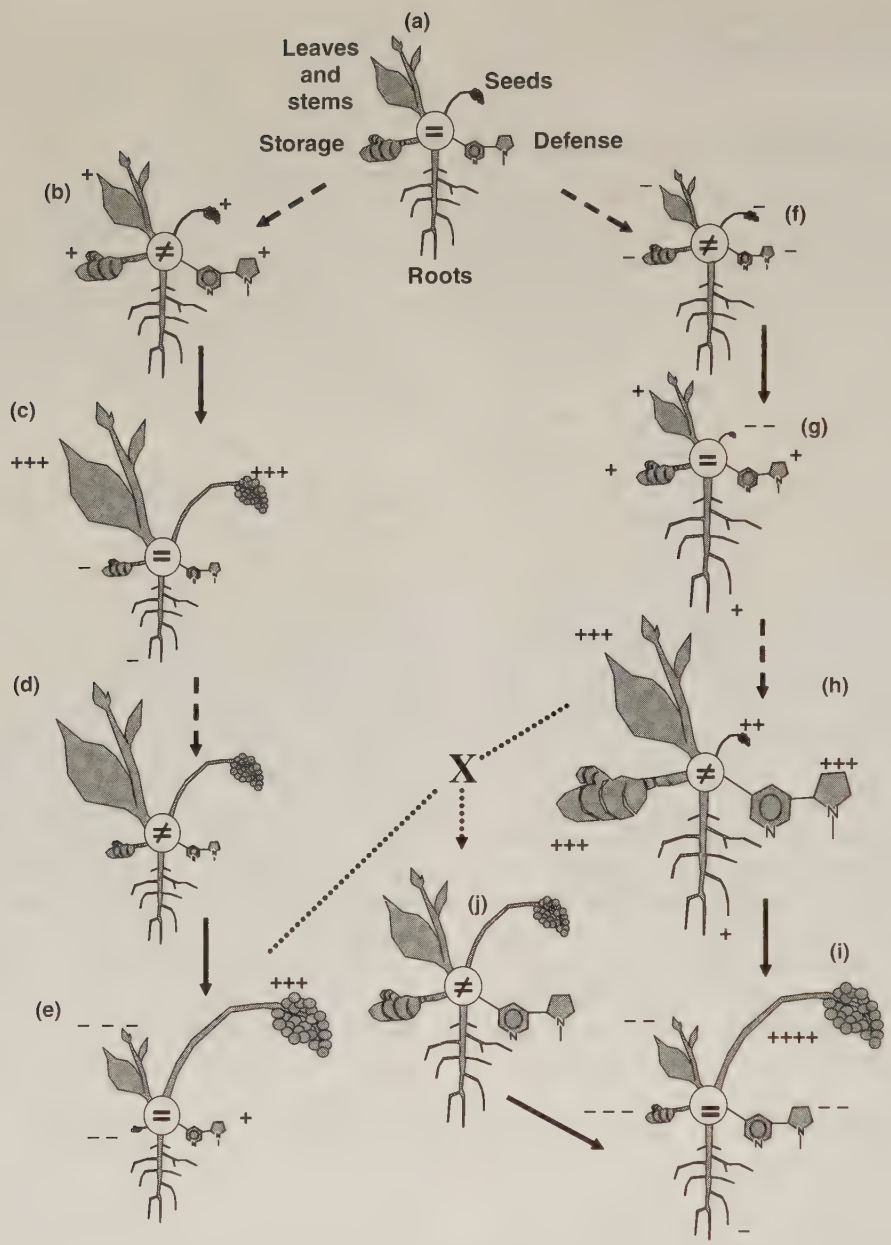

Figure 2. Relative increases (+) and decreases (–) in carbon allocation among seeds, storage, defense structures and compounds (Defense), leaves and stems, and roots due to environmental changes (solid arrows), selection (dashed arrows) and hybridization (dotted arrows) in the hypothetical domestication of annuals and perennials. Populations are in equilibrium (=) or disequilibrium (≠). The populations presented are: (a) a short-lived perennial in an environment with moderate resource availability and competition; (b) a weak perennial in an agricultural field; (c) an annual weed in an agricultural field; (d) a wild annual placed in a plant breeding nursery; (e) a domestic annual grain crop; (f) a weak perennial in a competitive environment; (g) a strong perennial in a competitive environment: (h) a wild perennial placed in a plant breeding nursery; (i) a domestic perennial grain crop; and (j) a hybrid between a wild perennial and a domestic annual, placed in a plant breeding nursery.

acted to maximize fitness, the population is now in disequilibrium.

Given time and natural selection pressure, the population may reach a new equilibrium, becoming an annual weed (Fig. 2c). Plants in disturbed habitats typically allocate reduced amounts of carbon to roots, storage organs and defense, because these are generally less important to a fast-growing annual plant experiencing low competition[22,46,47]. Carbon allocation to stems and leaves increases under selection pressure, to take advantage of the available resources[47], and finally, allocation to seeds typically increases because of the critical importance of seed to fitness in an annual plant[22] in a frequently disturbed (i.e., hazardous) environment.

Next, consider an annual weed that is to be domesticated as a new grain crop. Its morphology is initially unchanged, because environmental conditions are similar. But it is no longer an equilibrium population (Fig. 2d), because fitness

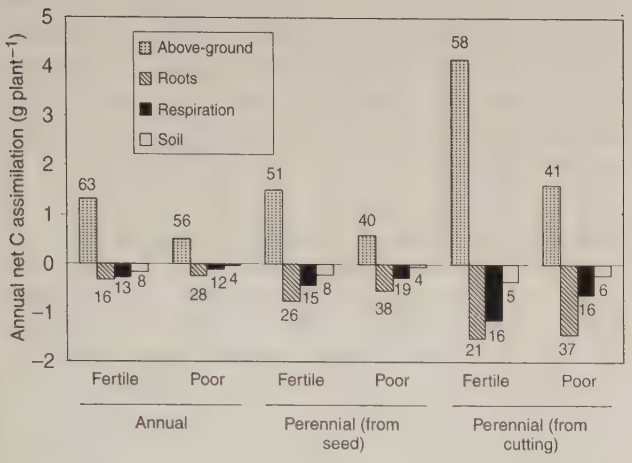

Figure 3. The relationship between nutrient availability and the partitioning of carbon assimilates in annual and perennial grain plants (data from Warembourg and Estelrich[45]).

is now defined by the plant breeder, who favors plants or families that produce maximum seed yields under high density.

The plant breeder's definition of fitness results in selection that produces an equilibrium population with high seed yield, adequate defense allocation and reduced allocation to stems and leaves (Fig. 2e). This population will avoid intense intraspecific competition[48], enabling it to be grown at a high density, as most modern annual crops are grown (Fig. 1c). Some allocation to vegetative storage is likely to remain as a means to tolerate stress[31].

Because modern varieties can have higher yields than landraces, even in low-fertility environments[49], plant breeders may be tempted to conclude that the trade-off concept does not apply to artificial selection. Modern wheat varieties seem to be a case in point, but they have the benefit of newly introduced yield, dwarfing and disease resistance genes that were not present in the original landrace equilibrium population. The expansion of available genetic diversity has allowed plant breeders to increase yield without producing readily identifiable trade-offs.

Even though the high-yielding crop in this model is an equilibrium population, future yield increases are not precluded. If the environment is changed via improved management, selection can once again be used to increase seed yield. Furthermore, additional genetic variation can arise from mutation or hybridization with other high-yielding varieties, landraces or related species.

Domestication and Breeding of Perennial Grains

There are two possible scenarios for the development of a perennial grain crop. First, we consider the evolution of a long-lived perennial. If the short-lived perennial starting population (Fig. 2a) is subjected to reduced resource availability due to increasing competition (Fig. 2f), its total growth is likely to be reduced. When nutrient availability is low (perhaps due to root competition), total carbon fixation is often reduced, and roots now require a greater proportion of available carbohydrate (Fig. 3) to obtain the limiting nutrients[44,45,50]. In this instance, resource scarcity refers to available rather than total resources. For example, soils can have high organic nitrogen content but little nitrogen available for plant growth.

Through natural selection, the population becomes adapted to its stable, highly competitive environment and is able to increase total carbon fixation relative to its unadapted condition (Fig. 2g). Under low resource availability, selection is expected to reduce allocation to seeds and increase allocation to structures that will increase competitive ability[21], such as roots, stems, defense and storage. A resource allocation strategy that improves the plant's survivorship will be likely to maximize its fitness in a competitive resource-scarce environment[28]. Although allocation to seed is reduced, this does not mean that seeds are of little value to the perennial. Rather, fitness is maximized by sustained production of smaller numbers of seeds per year.

A long-lived prairie plant placed in a plant breeding nursery would be likely to greatly increase growth and allocation to storage, defense, leaves and stems (Fig. 2h). Allocation to seed may increase only slightly, because the plant is genetically programmed for longevity rather than seed production in a single year. This pattern of greatly increased growth and above-ground allocation was observed when the perennial *Bromus madritensis* was grown on fertile compared to poor soil (Fig. 3).

Under the new environmental conditions of the breeding nursery, the population is now in disequilibrium and being selected for increased seed yield and longevity. After many selection cycles, the population attains equilibrium, with an average seed yield approaching that of annual crops (compare Fig. 2e and i). Compared with annual crops, however, there will be greater allocation to defense structures and compounds, because a long-lived perennial plant must be able to tolerate environmental extremes and defend itself against herbivores and pathogens, populations of which can build up over time. Although we expect the perennial grain to have a much larger root system than the annual grain (Fig. 1), proportional allocation to roots may not need to be much larger after the first year. For this to be true, annual respiration and root turnover in the perennial root system must not exceed the cost of building a complete root system in an annual. According to Weaver, root turnover in prairies is about 40% annually[51] and respiration can easily equal 50% of root mass annually (Fig. 3). Therefore, allocation below ground level will exceed that of annual crops unless the root systems of perennial grain crops are somewhat smaller (Fig. 1) or more efficient than in wild perennials. Net allocation to storage is modest because much of the stored photosynthate and nutrients can be remobilized in the following year. The resources stored by perennials can enable them to sustain seed production even in stressful conditions[52].

If a wild perennial has low seed yield, the time required for domestication will likely be long. If the species can be hybridized with a related domestic annual, interspecific crossing may speed perennial grain development. The hybrid is expected to have a resource allocation pattern that is intermediate to the two parents (Fig. 2j) because hybrids are generally intermediate in longevity, seed yield and allocation patterns[12,53]. Furthermore, the genetic variance for traits affecting both seed yield and longevity will increase over either parent, allowing more rapid progress in selection for yield and longevity simultaneously. The large genetic variance is beneficial because it is due to the presence of useful 'domestication alleles' from the crop and 'perenniality alleles' from the wild plant.

The development of a perennial grain crop should not be viewed as simple modification of an annual grain crop (Fig. 1c). The latter is fixing as much carbon as possible during its short lifespan and allocating as much of that carbon as possible to harvestable seed. Therefore, it cannot be expected to maintain the level of durable defense against pathogens and pests that is common in perennials, let alone store enough carbon to regrow in the following season. The high-yielding annual grain crop is an equilibrium population resulting from selection for seed yield. Because negative correlations between fitness components are the rule in equilibrium populations, selection for any other trait, including those that could increase longevity, must necessarily come at the cost of reduced seed yield.

Crossing the annual crop with a perennial species changes the genetic constitution, so that the progeny comprise a disequilibrium population, in which trade-offs are not necessarily fixed. A hybrid between the perennial and the annual crop may be able to acquire water and nutrients from greater depth throughout the year, and harvest light energy earlier in the spring and later in the fall. As a result, the perennial plant is able to fix more total carbon (Table 1, Fig. 3), which can be allocated to storage, below-ground allocation and defense. The trade-off of carbon among various functions is avoided if the total pool is increased in the more efficient perennial plant.

The framework also explains how high-seed-yielding herbaceous perennials could be developed through selection, despite their rarity in natural ecosystems. In their native, resource-scarce environments, where perennials have a competitive advantage over annuals, plants maximize fitness via allocation to roots, storage, leaves, stems and defense/tolerance. This allocation pattern increases competitive ability and longevity to maximize fitness. In contrast, a plant breeder can develop a perennial plant with reduced competitive ability by selecting for shorter stature, a less spreading root system, reduced tillering and more erect leaves.

It is important to remember that the allocation patterns arrived at in equilibrium populations (Fig. 2) are not necessarily the optimal allocation imaginable, but rather the optimal allocation possible for the population under consideration. If additive genetic variance for a trait, such as seed yield, is low, other traits that increase breeder-defined fitness may show a greater response to selection. Furthermore, strong negative correlations between traits can limit the ability of selection to increase fitness components simultaneously.

Promising Perennial Grain Programs

At the Land Institute, four perennial taxa are being domesticated and selected for grain production: intermediate wheatgrass, Illinois bundleflower, Maximilian sunflower (*Helianthus maximiliani*) and *Silphium* spp.[2,54]. A recurrent selection program to improve kernel size, yield per unit area and threshability of intermediate wheatgrass is under way. Hybridization methods for Illinois bundleflower, a species with no human-directed breeding history, are being developed in order to begin recurrent and pedigree selection. The sunflower and *Silphium* programs are at the initial germplasm evaluation stage.

With some of these and other species, there is an opportunity to combine grain production with perenniality through interspecific and intergeneric hybridization[2,54]. Work with amphiploids and backcrosses derived from crossing wheat (*Triticum aestivum* and *T. turgidum*) and triticale (× *triticosecale*) with three wheatgrass species (*Thinopyrum elongatum, Th. intermedium* and *Th. ponticum*) is under way, and initial crosses with members of the genera *Elymus, Leymus* and *Agropyron* are being made. By 2002, 1500 intergeneric hybrids between annual small grains and wild perennial relatives had been made, and by 2003 more than 600 progeny had been obtained by backcrossing or chromosome doubling to restore fertility. The wheat breeding program at Washington State University is evaluating more advanced perennial wheat germplasm[12].

The Land Institute's first hybridization project was to develop perennial sorghum from crosses between grain sorghum (*Sorghum bicolor*) and johnsongrass (*S. halepense*). Since 2001, we have been broadening the base of that perennial gene pool by crossing with newly released grain sorghum germplasm having superior grain quality. Crosses are also being made between annual, cultivated sunflower (*H. annuus*) and Maximilian sunflower (*H. maximiliani*), Jerusalem artichoke (*H. tuberosus*) and other perennial sunflower species with the intent to produce a perennial grain sunflower.

Development of perennial grains from the species and hybrids listed above will take several decades. A promising, shorter-term prospect for tropical regions may have been the International Rice Research Institute's (IRRI) perennial rice breeding program, which ran from 1995 to 2001. Yields of many of the hybrids were large, indicating good potential for perennial rice to exceed yields of 1000–2000 kg ha^{-1} in South-East Asian upland conditions[55]. Some of the most strongly perennial families had the highest grain yields, and there was not a negative

correlation (trade-off) between yield and survival. Particularly promising was the ability of the perennial hybrids to produce a dry-season crop, which could be extremely important to the welfare of farmers in South-East Asia. Researchers concluded that 'Breeding perennial cultivated rice should be feasible but it will likely take five to ten more years'[55]. Despite excellent prospects, the program was discontinued, primarily due to priorities within IRRI and lack of funds (Erik Sacks, personal communication, 2004).

Conclusions

The primary issue addressed in this paper is whether there exists solid evidence or theory demonstrating that an inevitable trade-off between perenniality and seed production precludes the breeding of perennial grain crops. The answer to this question is clear. Trade-off theory, when approached from a quantitative genetic perspective, does not rule out perennial grains.

Because perennial plants can be inherently more efficient and productive than annuals, resources may well be available for both grain production and perennation. The larger question of whether specific perennial grains such as sorghum, sunflower or wheat can be developed remains unanswered. This question depends upon a host of genetic factors and can be answered only by attempting to breed these perennial crops.

The potential benefits of perennial grains, in terms of soil conservation, reduced agricultural inputs and improved wildlife habitat are great, while the risks are comparatively modest. For example, breeding programs in numerous perennial grain species could be conducted using only a small fraction of the United States Department of Agriculture's annual budget. Indeed, several perennial grain breeding programs have been initiated and are progressing well. If progress is sustained and funding expanded, perennial grains could be widely available within decades.

For maximum benefit, perennial grain programs must be expanded and initiated in the immediate future. The process of breeding perennial grains will itself generate data crucial to the debate about a trade-off between yield and the perennial habit. A call for further theoretical discussion is therefore an argument for accelerating rather than postponing serious breeding efforts.

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Meeting the challenge of disease management in perennial grain cropping systems

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Abstract

Perennial grain production will likely present unique challenges for managing diseases that affect the productivity and longevity of crops being considered. Typical cultural practices effective at reducing soil- and residue-borne pathogens, such as annual crop rotations, delayed fall planting, and tillage, are not feasible in perennial systems. Consequently, soil- and residue-borne pathogens, and pathogens such as root colonizers and viruses that survive in live tissue, may increase in importance in a perennial grain crop. Resistance genes will undeniably be important defenses against disease. However, it is seldom, if ever, possible to incorporate within a single cultivar resistance to all existing and future important diseases. Furthermore, genes vulnerable to 'boom and bust' cycles are generally short-lived when deployed in monocultures. For these reasons, the use of mixtures of crop cultivars or species that vary in resistance functions will likely be an important strategy for managing diseases and pests of perennial grains. Burning of plant residue, a natural phenomenon in native perennial grass systems, may also be an effective disease management strategy. The successful implementation of these management tools may reduce or eliminate the risk that perennial grain crops will become pathogen refugia that affect neighboring annual plantings and the productivity of perennial plants.

Key words: perennial wheat, host diversity, mixtures, blends, polyculture, resistance, burning

Introduction: A Perennial Problem

One of the most critical issues facing the growing global human population is the maintenance of agricultural productivity[1]. Cereal grains provide more than 50% of human caloric needs, but problems associated with annual grain crops, such as soil erosion and degradation of water resources, indicate that reliance on annual grain production is a fundamental problem of current agricultural practice[2]. Successful production of perennial grains could profoundly reduce the adverse effects of agriculture[3,4].

Management strategies for a perennial grain cropping system may depend more on ecological principles governing natural ecosystems, hay meadows, and rangeland than those governing an annual grain crop. It will be important both to understand ecological principles and to understand the process of breeding and selecting high-yielding perennial lines. Plant pathogens will likely play an important role in the production and persistence of perennial crops. This paper reviews current knowledge relevant to management of diseases in a perennial grain cropping system, with emphasis on genetic resistance, host diversity, and burning. Included is a discussion of the potential challenges faced and perspectives from ecology. We highlight perennial wheat (*Triticum* spp.) and related cereals, although several other perennial crops are being considered in breeding programs, such as sorghum (*Sorghum* spp.), Illinois bundle flower (*Desmanthus illinoensis*) and sunflower (*Helianthus* spp.)[5]. Many of the concepts discussed here also apply to these other perennials, since the profile of pathogens infecting them is similar.

Perennial grain production will likely give rise to new disease management challenges. Cultural practices effective at reducing disease inoculum in annual systems, such as crop rotation, delayed fall planting, and tillage, are not feasible in perennial systems. In a no-tillage system, crop residue persists at the surface and subsurface soil layers,

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providing a refuge for survival of pathogens between seasons. Similarly, live roots and crowns persisting in soil can harbor pathogens that require live tissue for survival, such as viruses and root-colonizing pathogens. Observations in Kansas, USA, of perennial progenitors, such as intermediate wheatgrass (*Thinopyrum intermedium*) and sorghum, show that these plants are emerging and assimilating carbon well before their annual counterparts (see DeHaan et al., this issue). This lengthening of the growing season provides more opportunities for pathogenic relationships and greater potential for affecting other nearby crops. Meeting the challenge of managing diseases and pathogen populations in a perennial grain crop is, therefore, important for grain production and stand longevity.

Conversion from Annual to Perennial: Potential Impacts on Disease

A consideration of disease epidemics likely to arise in perennial wheat production provides a useful starting point for addressing potential problems in other perennial crops. In annual wheat (*Triticum aestivum*) production, many diseases are managed in part by cultural practices that disrupt the disease cycle (e.g., tillage, rotation and delayed seeding). Such diseases may pose significant problems for perennial wheat, characterized by low disturbance and stand persistence over multiple growing seasons. Disease problems of continuous, no-tillage annual wheat, in particular, provide insight into disease challenges likely to be faced by perennial wheat. As in the case of no-till annual wheat production, soil- and residue-borne pathogens may thrive under perennial wheat production, as well as pathogens, such as root colonizers and viruses, that survive in live tissue. In addition, the ability of the pathogen to compete in the soil or on plant residue as a saprophyte must also be considered. Various pathogen characteristics, therefore, can be used as predictors for increased disease problems under perennial wheat production in the Great Plains: survivability between crops in host residue, soil, or live tissue; high saprophytic competitiveness on colonized crop residue; the ability to infect older roots; and whether or not the disease is typically managed in part through delayed planting and tillage. The presence of any of these characteristics may indicate increased disease potential (Table 1), assuming limited resistance, although one characteristic may prove to be more important than another.

Before making assumptions about disease potential, the differences in root systems between a perennial plant and an annual plant must be understood. Annual wheat roots (Fig. 1) live for a fraction of the year, with 62%[6] to 90%[7] of the total root mass located in the upper 0.3 m of soil. Roots of perennial relatives (Fig. 1) extend much deeper into the soil profile, have greater biomass[8,9], and are present throughout the year. Additionally, more complex crowns may act as a barrier to soil-borne pathogens, even in the absence of resistance genes (i.e., receptors). For example, Mathre and Johnston[10] demonstrated that movement of *Cephalosporium gramineum* was slower through roots and crown tissues of *Thinopyrum elongatum* and *T. intermedium* than those of wheat lines, and therefore, suggested that a more complex crown structure contributed to Cephalosporium stripe resistance in these perennial species.

Thick, healthy perennial grass stands, like those established on Conservation Reserve Program land, reduce soil erosion[11], restore soil nutrient levels and organic matter[12], increase soil quality[13], and increase soil microbial activity[13] and diversity[14]. The ability of soils to generally suppress soil-borne diseases is often enhanced by the addition of organic matter, the build-up of soil fertility, and certain agronomic practices such as no-till[15,16], all of which potentially increase soil microbial diversity and activity. Consequently, competition shifts between pathogenic, beneficial, and saprophytic organisms may compromise the dominance or fitness of those pathogenic on the host. For example, differences were found in the diversity of several microbial groups between permanent grassland and arable cropland under rotation, and the evenness of ecophysiologically differing bacterial types was higher in grassland[17]. Further, growth of the root rot fungus *Rhizoctonia solani* AG3 was suppressed more in grassland than in arable soils. Earthworms, often more abundant in undisturbed soils[14], also decrease the effects of some soil-borne diseases, including take-all (caused by *Gaeumannomyces graminis* var. *tritici*)[18]. Indeed, it has been suggested that indicators for soil health may be indicators of a soil's ability to suppress disease caused by root pathogens[19].

Disease-suppressive soils, in which indigenous microflora effectively protect plants against soil-borne pathogens, have been described for many soil-borne pathogens. This phenomenon depends on plant species, the disease in question, soil properties, and agronomic practices. Perhaps the most thoroughly studied example of soil suppressiveness, the decline of take-all spontaneously occurs in monocultures of susceptible wheat after 4–6 or more years of continuous cropping[16]. The build-up of antagonistic soil microbes, with fluorescent pseudomonads specifically implicated worldwide, is associated with take-all decline. Wheat, *T. intermedium, T. elongatum*, and several perennial grain germplasm lines are susceptible to take-all (C. Cox et al., unpublished data) and if present in a perennial wheat crop, take-all would most likely decline as well. For example, as bacterial populations change within brown patches of turfgrass infected by *G. graminis* var. *avenae*, take-all declines and susceptible species can recolonize formerly diseased areas[20].

The take-all pathogen is a weak competitor in communities of saprophytes in plant residue[21]. Some of the dominant grasses of the tall and short grass prairies have no resistance to take-all (C. Cox and Garrett, unpublished data), although it may be that the established microbial community in the prairie ecosystem has a suppressive effect on take-all. *Cephalosporium gramineum* produces broad-spectrum fungal antibiotics that are thought to

Table 1. Common wheat diseases of the Great Plains, and pathogen characteristics as predictors of disease potential in a perennial wheat cropping system.

	Characteristic[1]					
Disease	**Survives between crops in host residue or soil?**	**Competes well on residue or in soil?**	**Affects older roots?**	**Survives between crops in live tissue?**	**Increased with early fall planting date?**	**Worse with reduced tillage?**
Wind-borne, leaf-infecting						
Leaf rust	–	N/A	–	+	–	–
Stripe rust	–	N/A	–	+	–	–
Stem rust	–	N/A	–	+	–	–
Powdery mildew	+	+/–	–	–	–	+
Flower-infecting						
Scab	+	+/–	–	–	–	+
Bunt and loose smut	–[2]	–	–	–[3]	+	–
Viruses						
Wheat streak mosaic	–	N/A	–	+	+	+
Barley yellow dwarf	–	N/A	–	+	+	–[4]
Soilborne mosaic	+	+	–	–	–	–
Soil- or residue-borne						
Tan spot	+	+/–	–	–	–	+
Septoria	+	+/–	–	–	–	+
Take-all	+	–	+	+	+	+
Cephalosporium stripe	+	+/–	–	+	+	+
Common root rot, dryland foot rot	+	+/–	+	–	+	–[4]
Strawbreaker foot rot	+	+/–	–	–	+	–[4]
Pythium root rot	+	+	–[5]	–	–	+

[1] +, Pathogen or disease has the characteristic, so increased disease potential is more likely with conversion from an annual to a perennial wheat cropping system assuming limited resistance. –, Pathogen or disease does not have the characteristic, so increased disease potential is less likely with conversion from an annual to a perennial wheat cropping system. +/– refers to an intermediate response. N/A = characteristic not applicable to the disease.
[2] Sometimes survives in soil as spores.
[3] Spores or mycelium associated with dormant seed.
[4] Disease decreases in reduced tillage.
[5] Infects young roots.

exclude the more aggressive saprophytes from the substrate[22,23]. The competitive saprophytic ability of *C. gramineum* may, therefore, make it more problematic on perennial wheat than the take-all pathogen.

Above-ground organs of perennial grasses may appear similar to seedlings during fall or spring regrowth, yet there are substantial, more mature plant roots and crowns present below ground throughout the year (Fig. 1). Root pathogens such as *Pythium* and *Rhizoctonia* are classic problems in no-till systems and may also be significant on perennial wheat seedlings, especially during the establishment stage. Juvenile roots are particularity susceptible to infection and attack at the seedling stage can be devastating for plants[24]. Mature plants, including older perennials, can also be adversely affected by root pathogens[25], especially since perennial plants continually replace old roots with new feeder roots.

For wind-dispersed, host-specific foliar pathogens, such as rusts and powdery mildews, there is ample evidence that mixing resistant host genotypes with susceptible genotypes

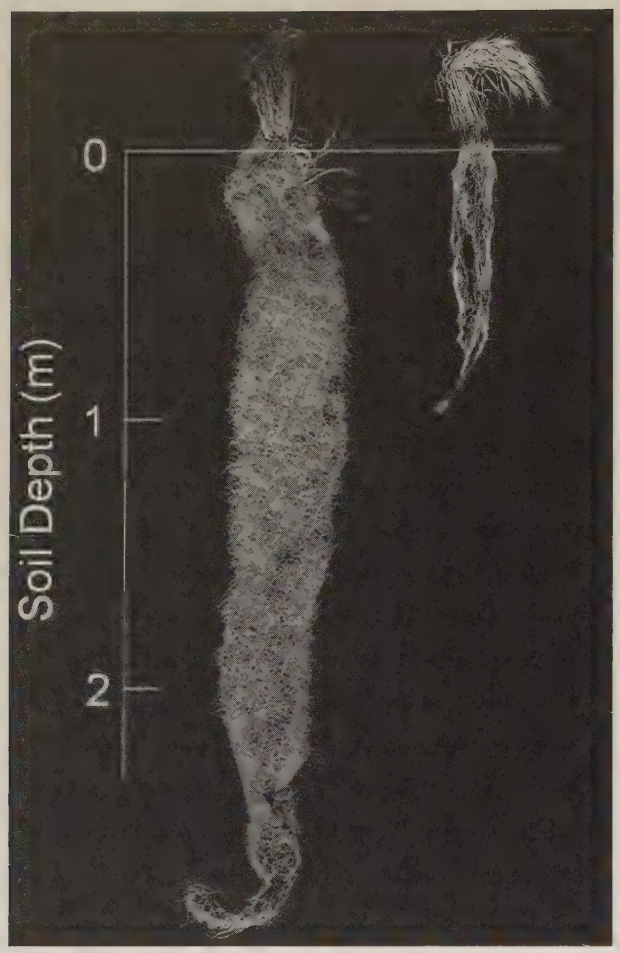

Figure 1. An illustration of the potential difference in root architecture between annual wheat and a perennial relative of domesticated wheat. The roots on the right are from the annual winter wheat cultivar Karl 92 and the roots on the left are from *Thinopyrum intermedium*. Plants were grown outdoors in 3 m long cylinders under similar growing conditions and excavated in late June. (Photo courtesy of Scott Bontz, The Land Institute, Salina, Kansas, USA.)

effectively reduces disease severity[26–31]. In addition, such mixtures of genotypes may increase the durability of major gene resistance[31,32]. Since inoculum of *Puccinia* species (the rust pathogens) seldom overwinters in much of the Great Plains, conversion from annuals to perennials may not affect these diseases. However, because the survival structures (ascocarps) of powdery mildew fungi survive between crops in and on plant residue, long-term effects of pathogen persistence should be considered when managing powdery mildew under a perennial production system.

Unforeseen minor diseases may become prevalent with the introduction of new perennial germplasm. Additionally, any dramatic shift in the microclimate, due to conversion from an annual to perennial grain crop, can have a significant positive, neutral, or negative impact on pathogens and disease development[33].

It is clear that perennial grain production will present challenges for disease management. But in typical agricultural environments, disease pressures are a reality in any crop, whether annual or perennial, and may greatly limit yield potential and management strategies. Many crops are grown successfully even though significant disease problems exist. Disease epidemics of annual wheat remain common despite decades of focused research to prevent outbreaks. Although disease reduces average annual wheat yields in Kansas by more than 13% each year[34], Kansas remains the leading wheat producer in the nation. Herbaceous perennials such as Kentucky bluegrass (*Poa pratensis*), switchgrass (*Panicum virgatum*), and alfalfa (*Medicago sativa*) are also important agricultural crops, despite disease and pest problems.

Resistance, Gene Deployment and Durability

Although ecological studies are, and will be, sorely needed to further examine pathogenic relationships in a perennial grain crop, development of genetic resistance to economically important diseases through plant breeding programs is necessary. Wild plants with inherently slow growth rates, such as most perennials, tend toward large investments in antiherbivore defense compared to plants with fast growth rates, such as most annuals[35,36]. A limited number of studies have also compared annual versus perennial life histories in terms of pathogen defense. For example, in response to six maize viruses, three annual teosinte (*Zea* spp.) lines were susceptible to all of the viruses, whereas perennial diploid and tetraploid teosintes were each susceptible to only one of the six viruses[37]. These differences in susceptibility probably developed because perennial plants have evolved in the context of longer-term exposure to pests and pathogens in natural ecosystems than have annual plants. Despite this greater exposure, perennials dominate most native landscapes and constitute roughly 80% of North America's native flora[38]. In other words, the pressure of disease has not led to the downfall of perennials.

Wheatgrasses (*Thinopyrum* spp.), the wild relatives of modern wheat, and hybrids of wheatgrass × wheat show high levels of resistance to many common wheat diseases, including Cephalosporium stripe, wheat streak mosaic (and its wheat curl mite vector), stripe, stem and leaf rust, barley yellow dwarf, eyespot[39–43] and tan spot (C. Cox and Garrett, unpublished data). Indeed, finding *Thinopyrum* lines highly susceptible to common cereal diseases for purposes of ecological studies has been challenging (C. Cox, personal observation).

Resistance to diseases in natural systems is often heterogeneous within plant populations and dynamically coevolves with virulence genes in the pathogen population. For example, in the Fertile Crescent where oat (*Avena* spp.) and oat crown rust diversity are high, only 30% of individuals within populations tested were resistant to oat crown rust[26]. In populations of *Linum marginale*, an herbaceous perennial flax found abundantly in Australia,

patterns of resistance varied with patterns of virulence in the associated populations of the rust pathogen *Melamspora lini*[44,45]. Broadly virulent pathogens dominated highly resistant host populations, whereas weakly virulent, more aggressive pathogens dominated susceptible populations. In other words, in the susceptible host populations, rust pathogen isolates had few virulence genes that could overcome specific plant defense and allow disease to occur (virulence), but were highly fit and capable of causing high disease severity on the plant genotypes they could infect (aggressiveness). Aggressiveness was most likely mediated by among-pathotype competition and favored over virulence in susceptible host populations. On the other hand, greater virulence, or the ability to infect multiple host genotypes, was favored over aggressiveness in resistant populations. Part of this explanation relies on the assumption that there is a cost to carrying extra virulence genes.

In agriculture, host-plant genetic resistance is not always available for every potential disease, and it is difficult to incorporate resistance genes that target all specific pathogen populations into a single crop cultivar. Further, genes deployed in monocultures of single cultivars may be more vulnerable to 'boom and bust' cycles. The numerous examples of defeated major gene resistance are evidence that 'selection [for pathogen virulence] is efficient in agricultural ecosystems that are based on monoculture and genetic uniformity'[32]. Deployment of a major resistance gene specific for a virulence gene in the pathogen population in monoculture over a large geographical area imposes a change in the selection pressure within the pathogen population. Mutant (or migrated) virulence alleles not recognized by the resistance genes are favored, thus the frequency of virulence increases over time and resistance breaks down[32]. The coevolutionary arms race between resistance genes in host populations and virulence genes in the corresponding pathogen populations also occurs in natural ecosystems and predates agriculture.

McDonald and Linde[32] suggest four characteristics of a pathogen that pose the greatest risk for defeating resistance genes: both sexual and asexual reproduction, high potential for genotype flow, large effective population sizes, and high mutation rates. Mixtures of different crop cultivars or species, among other noteworthy methods such as gene pyramiding and gene rotation, may disrupt directional selection, so that the rate of increase of pathogen mutant alleles or genotype frequencies slows[31,32]. However, wide-scale deployment of a single mixture comprised of only a few component genotypes could also ultimately prove to be undesirable in terms of pathogen selection pressures, major gene conservation, and effective disease control[31].

Host Diversity and Lessons from the Ghost of Disease Past

Increased diversity at one trophic level often begets increased diversity at other levels[46]. For example, an increased number of plant species in a community is frequently correlated with an increased number of insect species[46–48]. Similarly, more diverse pathogen populations are found in natural ecosystems where plant diversity is high, compared to monocultures in conventional agroecosystems[26,31,49]. Pathogen diversity even increases in mixtures of annual grains[31]. Thus, not only can perennial roots increase soil microbial diversity, as previously discussed, but increasing plant species or genotype diversity can also increase microbe and insect diversity.

The accumulation of detrimental pathogens in plant rhizospheres can affect both annuals and perennials in natural and agroecosystems. In natural ecosystems, the build-up of pathogens can profoundly affect plant community structure. At the plant population and community levels, this interaction may alter host-plant competitive abilities, facilitate existence of tolerant or non-host-plant species, and prevent domination of strong competitors[49–53]. As a result, these plant–pathogen relationships may facilitate successional processes, enhance genetic diversity and structure of host populations, and maintain plant (and pathogen) biodiversity in natural ecosystems. From the perspective of a plant pathologist working on agronomic problems, pathogen build-up seems natural in any plant stand, especially perennials. However, lessons from plant ecology suggest that the problems of genetic uniformity may become too great within a perennial cropping system. Indeed, Harper[54,55] concluded, 'host specific pathogens appear to penalize a population that becomes dominated by a single species', and therefore, 'diversity in plant communities may reflect the failure of pure stands'. This phenomenon is often described as 'the ghost of disease past'. Mitchell et al.[56] estimated the effects of different plant species diversity levels on foliar fungal diseases in grassland plant communities, and observed that for the overwhelming majority of the diseases evaluated, decreased plant species diversity increased pathogen load. Increasing host diversity in a perennial cropping system may increase the resilience and resistance to attacks by pests and pathogens.

The ability of small-grain cultivar mixtures to substantially reduce the severity of foliar disease caused by polycyclic, specialized, wind-dispersed pathogens, such as rusts, powdery mildews and rice blast, has been well demonstrated[26–31,57–59]. Infection by viruses may also be reduced in grass mixtures if the pathogen population is partitioned between grass types, or if vector behavior changes markedly. For example, barley yellow dwarf virus (BYDV) infects three major prairie grasses, but the dominant virus strains appear to differ among these species and also to differ from the dominant wheat strain[60]. Further, aphid vectors of BYDV exhibited shorter feeding times in oat mixtures compared to oat monocultures, with associated lower rates of virus transmission[61].

Additional study is needed to better understand the effects of mixtures on soil-borne, monocyclic and/or splash-dispersed pathogens. Collectively, results of these empirical studies are less consistent[31,59,62–66]. Garrett and

Table 2. Common wheat diseases of the Great Plains and inherent characteristics of host–pathogen system as predictors of host-diversity effect for reduced disease.

	Characteristic[1]			
Disease	**Shallow dispersal gradient**	**Small lesion size**	**Many pathogen generations per epidemic**	**Strong host specialization**
Wind-borne, leaf-infecting				
Leaf rust	+ +	+ +	+ +	+ +
Stripe rust	+ +	+	+ +	+ +
Stem rust	+ +	+	+ +	+ +
Powdery mildew	+	+	+ +	+ +
Flower-infecting				
Scab	+/−	−	−	−
Bunt and loose smut	− −	− −	− −	+ +
Viruses				
Wheat streak mosaic	+/−	− −	−	−
Barley yellow dwarf	+ +	− −	−	−
Soil- or residue-borne				
Soilborne mosaic	− −	−	− −	+/−
Tan spot	+/−	+/−	+/−	+/−
Septoria	+/−[2]	+/−	+/−	+/−
Take-all	− −	−	− −	−
Cephalosporium stripe	− −	− −	− −	−
Common root rot, dryland foot rot	− −	+/−	−	−
Strawbreaker foot rot	−	−	−	+
Pythium root rot	− −	+/−[3]	+/−	− −

[1] + +, Pathogen system strongly exhibits the characteristic, so a host-diversity effect of reduced disease is most likely. +, Pathogen system exhibits the characteristic, so a host-diversity effect of reduced disease is more likely. −, Pathogen weakly exhibits the characteristic, so a host-diversity effect of reduced disease is less likely. − −, Pathogen system does not exhibit the characteristic, so a host-diversity effect of reduced disease is even less likely. +/−, Pathogen system moderately exhibits the characteristic.
[2] Dispersal gradient is initially shallow at the origin of the epidemic, but steep in subsequent cycles.
[3] Lesion size is relatively small on older roots and large on young roots and seeds.

Mundt[67] suggest that the effects of host diversity depend on the life history of the pathogen and will tend to be greatest when the host genotype unit area is small, there is strong host–pathogen specialization, the pathogen's dispersal gradient is shallow (i.e., inoculum levels drop off after relatively long distances versus a steep gradient in which inoculum levels drop off after relatively short distances), characteristic lesion sizes are small, and the number of pathogen generations over an epidemic is large. Using these criteria, diseases can be compared according to the magnitude of host diversity effect predicted (Table 2).

Wheat has a relatively small host genotype unit area–defined as the area occupied by an independent unit of host tissue of the same genotype[68]—compared to sorghum, corn and Illinois bundle flower. Wind-dispersed pathogens are often more effectively reduced in mixtures than splash-dispersed pathogens, probably due to the shallower dispersal gradients of the former. A shallower dispersal gradient tends to result in more movement of propagules away from the susceptible host plant, provided that an influx of inoculum does not saturate a field[67]. In light of these assumptions, cultivar mixtures would be expected to have less effect (over one growing season) on diseases that are monocyclic, splash-dispersed and/or soil-borne, compared to highly specialized, wind-borne diseases such as leaf rust and powdery mildew.

As a test of this hypothesis, the relative effectiveness of wheat cultivar mixing for tan spot versus leaf rust was

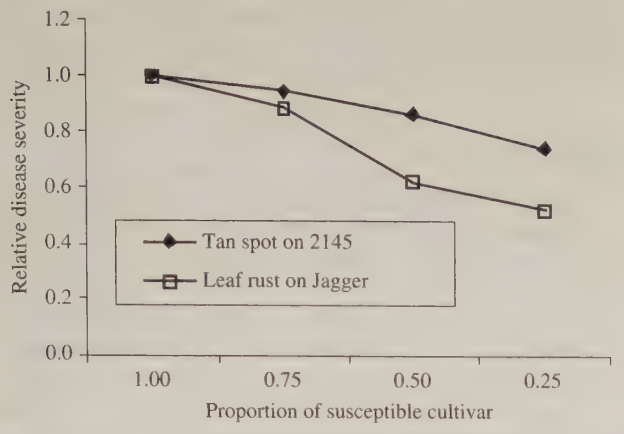

Figure 2. Relative effects of cultivar mixtures for leaf rust and tan spot on susceptible annual wheat cultivars, Jagger and 2145, respectively. This illustrates the greater effectiveness of mixtures to reduce severity of leaf rust compared to tan spot. Means combine site–years and treatments inoculated with both leaf rust and tan spot or either leaf rust alone (Jagger) or tan spot alone (2145). Relative disease severity of each mixture is expressed as a proportion of the severity in the monoculture of the susceptible cultivar. The two slopes are significantly different ($P < 0.0001$). (Reproduced from C. Cox et al., 2004[59].)

directly compared in a four site–year field experiment[59]. In contrast to leaf rust, a highly specialized, wind-borne pathogen with a shallow dispersal gradient, tan spot is residue-borne with a steep dispersal gradient[69]. Two annual wheat cultivars, one resistant to leaf rust and the other resistant to tan spot, were mixed in different proportions of 0.25, 0.50, 0.75 and 1.00 and inoculated with each pathogen alone and in combination. For both tan spot and leaf rust, disease severity decreased substantially on the susceptible cultivar as the proportion of that cultivar decreased in mixture. However, as predicted, mixtures were significantly more effective at reducing severities of leaf rust than tan spot (Fig. 2), supporting the above premise. In the absence of resistance genes, it may be that a better method of reducing soil- and residue-borne diseases is by increasing the diversity of soil microorganisms and saprophytes on plant residue. This would potentially facilitate competition between microbes and reduce the risk of a small number of pathogens dominating and, therefore, proliferating. In a perennial crop, this could be accomplished by increasing the diversity of perennial plants beyond two or three cultivars of the same species, so that the biological differences among plants effectively cultures diverse microbial communities. Perhaps the perennial nature of the roots may be an advantage when considering this objective[14].

Although much research with mixtures focuses on annual grain hosts, we do not expect disease responses within mixtures of perennials to differ from annual mixtures within a single growing season. However, the relationship between a perennial wheat crop and its pathogens is on a different temporal scale than an annual crop. An epidemic affecting an annually planted or rotated crop is generally short-lived and over when hosts are dead, or in less than 1 year. On the other hand, an epidemic could potentially affect a perennial crop over its lifetime, spanning many years. Depending on host-plant susceptibility and environmental conditions, this potentially increases the number of generations of pathogens that survive on host-residue over the duration time of the epidemic (which could be years) on the perennial crop compared to an annually planted crop. With more pathogen generations per epidemic, the ability of mixtures to reduce disease may increase over time (Table 2), provided the field does not become saturated with inoculum. This means that mixtures could have a greater effect on some diseases in perennial grain systems than in annual systems. This could hold especially against pathogens that have relatively few generations per year, such as many of the soil- and residue-borne and splash-dispersed pathogens. An experiment is in progress testing this hypothesis, using different biculture combinations of susceptible and resistant cool-season perennial grasses and alfalfa, and different epidemic ages (C. Cox and Garrett, unpublished data).

Determining the necessary level of diversity of cultivar or species mixtures, and the manner in which mixtures are best deployed for effectively reducing disease, is a complex task. Several factors influence the relative effectiveness of diversity, including the levels of resistance available, the environment, the disease in question, and the agronomic goals of the grower. Small increases in host diversity within annual wheat populations, such as two cultivar mixtures in which one cultivar is resistant to a disease, have substantially reduced the effects of disease[59]. In Kansas, mixtures consisting of 2–3 different cultivars covered 7% of the wheat acreage in 2001, 11.5% in 2002, and 12.8% in 2003, according to the Kansas Agricultural Statistics Service. Intercropping of two or more species is also desirable if there are no cultivars available within a species resistant to a particular disease, and may be important in a perennial grain crop. Also, increased diversity within a perennial grain cropping system may be desirable for reasons that go beyond the scope of plant pathology, such as more efficient moisture and nutrient management (see Crews, this issue).

Fire

Thus far, resistance and host diversity have been suggested as disease management tools in a perennial wheat cropping system. However, increased plant diversity may not be highly effective against every disease, especially those caused by pathogens that are relatively immobile, such as residue- and soil-borne pathogens (Table 2). Burning of the tallgrass prairie in the Great Plains is common and can increase plant productivity and affect plant community structure[70]. Burning is also well-known to increase seed yields of Kentucky bluegrass and other perennial grasses produced for seed. At this time, effects of fire on grain yield of wheatgrass and related perennial wheat materials is not

known, although potential increases in yield are possible by appropriate timing and frequency of burning. Limited research also suggests that burning can decrease disease potential by decreasing the amount of infested plant litter that would otherwise serve as inoculum sources. Burning decreases severity of Phoma and Ascochyta blights in alfalfa seed production fields[71], stripe rust in Kentucky bluegrass seed production fields[72], ergot in perennial ryegrass cultivation[72], rice stem rot[73], rice sheath blight[71] and Cephalosporium stripe of wheat[74]. Studies in the tallgrass prairie of Kansas also suggest that leaf rust is less common on *Erigeron strigosus* in annually burned sites compared to unburned sites (Dendy and Garrett, Dept. of Plant Pathology, Kansas State University, personal communication, September 2004). Although burning is largely prohibited in the Pacific Northwest, where perennial wheat is also being considered[42,75], fire may prove a critical tool in managing diseases of perennial grain crops in the Great Plains.

In addition to burning, grazing by cattle and bison in the tallgrass prairie is also important for plant productivity and maintenance of species biodiversity[70]. Rotational grazing may prove a critical tool in the productivity of perennial grain crops, and it would be worthwhile to examine its impact on disease and grain yields.

Conclusions

Sustainable disease management in perennial grain systems will require both the application of ecological principles and breeding expertise. The use of host genetic resistance to disease, host diversity, and field burning may prove critical management tools. Breeding for perennial species is a time-consuming, laborious task, and the release of suitable cultivars is still perhaps 25 years away. In the meantime, germplasm must be continually evaluated for disease resistance, among other agronomic traits, including perennial habit. Therefore, more ecological disease studies are needed, using perennial germplasm or analogues that examine resistance gene deployment in plant populations, host diversity, pathogen and microbial diversity, burning and rotational grazing. Additionally, lessons from plant ecology and the ghost of disease past must not be ignored. Understanding the cropping system as an ecosystem is important, perhaps more so when considering the management of perennial crops.

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Perennial crops and endogenous nutrient supplies

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Abstract

Perennial cropping systems may achieve significant improvement over annual systems in the synchrony between crop nutrient demands and nutrient supplies. Improvements in nutrient synchrony would result in the reduction of nutrient losses and their associated environmental impacts. A perennial system with high levels of synchrony would also require fewer nutrient inputs, such that it may be possible to develop an agriculture that functions mostly, if not entirely, on nutrient inputs from endogenous sources (i.e., weathering of primary and secondary minerals and biological nitrogen fixation). In this paper I describe three realms of research that will inform the development of relatively high-yielding grain production systems grown on endogenous nutrient supplies: (1) improvement of nutrient synchrony through the development of perennial crops; (2) identification of soils that are in a high nutrient release phase of pedogenesis, which could balance the export of rock-derived nutrients in crop harvests; and (3) optimization of legume density, harvest index and percent nitrogen derived from the atmosphere (%Ndfa) to achieve adequate nitrogen inputs through biological fixation.

Key words: legume, lithophilic nutrients, nitrogen, nitrogen fixation, pedogenesis, phosphorus, sustainability, synchrony, weathering

Introduction

It is often surprising for students of agriculture to learn that some of the most productive terrestrial ecosystems on Earth—the tropical rainforests—often grow from the most highly weathered and thus least fertile soils[1,2]. How is this possible? Simply put, a wide array of nutrient cycling mechanisms[3,4] prevent nutrient losses from exceeding what are often very low levels of nutrient inputs, thus allowing for high levels of photosynthesis to take place. When tropical rainforests that exist on highly weathered soils are cleared and burned for annual crop production, it is common for farmers who do not rely on fertilizer inputs to obtain only one or two years of harvests before soil nutrient deficiencies profoundly limit crop growth[5]. Crop productivity cannot be sustained primarily because the annual crops lack the extensive and morphologically diverse root systems and associated organisms that prevent the perennial tropical forest vegetation from leaking nutrients. Moreover, nutrients are exported from the annually cropped ecosystem in the harvest and are usually not returned in human manure.

The same eventual limitation of crop productivity caused by excess nutrient loss via leaching, runoff, gas fluxes and harvests was also commonplace in traditional agricultures of regions with less weathered soils[6,7]. In less-weathered temperate soils, gradual mineralization of nutrient-rich soil organic matter was responsible for longer lags between the initiation of annual crop production and the appearance of intense nutrient limitation. Once soil microbial respiration approached equilibrium with net primary production (NPP) in crop residues, however, nutrient losses (via harvests, leaching, runoff and/or denitrification) from annually cropped systems typically exceeded the relatively low background rates of natural nutrient regeneration.

In response to nutrient limitation encountered in annual cropping systems, traditional farmers of many cultures developed sophisticated, site-specific management strategies that effectively concentrated nutrients in time and/or space. An example of a farming system that concentrates nutrients in time would be a fallow rotation where nutrients are taken up and stored in fallow vegetation. When the fallow site is once again used for crops, the one or more years of 'banked' nutrients in the fallow vegetation are released through decomposition and made available to crops. An example of traditional farmers concentrating nutrients in space can be found in floodplain agriculture, such as that which occurred in the Nile River valley before the Aswan Dam[8]. Essentially, nutrients and nutrient-rich particles of silt, clay or organic matter are transported from

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large watersheds via leaching or runoff, into relatively small plots of land in the floodplain below.

During the twentieth century, traditional fertility management strategies in many cultures gave way to the modern practice of applying highly concentrated forms of essential crop nutrients. While highly successful at addressing nutrient limitation, synthetic fertilizers, particularly nitrogen (N), have now come under considerable scrutiny because of the detrimental ecological consequences of nutrient losses from agriculture; these include stratospheric ozone destruction, greenhouse gas production, freshwater and marine eutrophication and, in some cases, hypoxia, as well as threats to human health[9–11]. Moreover, N fertilizers, in particular, are very energy expensive to produce, usually comprising the greatest commercial energy input into modern production agriculture[12]. While annual grain-producing agroecosystems developed over the past 50 years have been highly successful at raising food productivity, dependence on non-renewable resources, and ecological impacts, cast serious doubt on their long-term sustainability.

In spite of its shortcomings, there exist few viable alternatives to annual crop production in general, and grain production in particular. One alternative—a perennial grain-producing polyculture—has been investigated by researchers at the Land Institute in Salina, Kansas. They have based their design of a perennial polyculture on taxonomic and functional groups that they observed in the native tallgrass prairie of central and eastern Kansas. The polyculture consists of a warm-season grass, a cool-season grass, a sunflower and a legume[13]. While it has been the goal of the Land Institute to develop a cropping system that, like the prairie, maintains productivity on inputs from atmospheric deposition, biological N fixation and soil mineral weathering, the question remains: Is it possible for a grain-producing agroecosystem to be both high yielding and continuously productive while relying on endogenous nutrient supplies? In this paper, I present a framework, based in part on research conducted in native ecosystems, to begin to address this question. I describe three considerations, and ultimately research directions, that I believe to be cardinal for a grain-producing agroecosystem to approach or achieve continuous high yields while relying on endogenous nutrient supplies:

1) Improvement in synchrony between rates of nutrient availability and crop demand.
2) Identification of soils that are in a 'high nutrient release' phase of pedogenesis or soil development.
3) Optimization of legume density, harvest and %N derived from the atmosphere (%Ndfa).

Improvements in Nutrient Synchrony

Nutrient synchrony is defined as the matching of crop demands for nutrients with nutrient supplies, either from organic or inorganic sources[14]. Annual, high-input

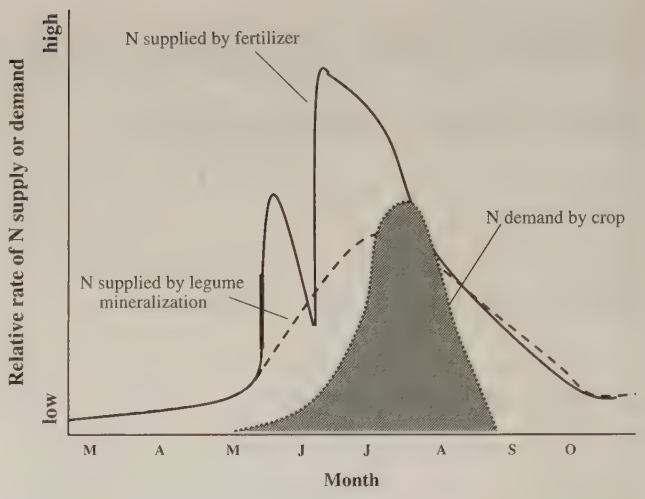

Figure 1. Asynchrony of crop demand (. . .) for nitrogen (N) and N supply via a split application of fertilizer (——) and legume residue mineralization (– – – –) in a hypothetical north temperate annual cropping system[16,17].

agriculture currently achieves low levels of nutrient synchrony, with only 30–50% of applied N fertilizer and 45% of applied phosphorus (P) fertilizer actually being taken up by crops[15]. This striking and important asynchrony can be largely explained by the absence of a proportionate sink or demand for fertilizer-supplied nutrients during most of the year. The high concentrations of nutrients that are applied as fertilizers at the beginning of a cropping cycle are susceptible to leaching, runoff and, in the case of N, denitrification and ammonia volatilization (Fig. 1)[16,17]. Nutrients remaining after a cropping cycle or mineralized from crop residues during fall or winter, are also susceptible to loss. While there is some evidence that under conventional management practices N supplied to crops via legume residues may be less vulnerable to leaching or gaseous loss than fertilizer N[18], rarely do either legume-based or fertilizer-based annual agricultural systems exceed levels of N synchrony greater that 60%, even when best management practices are employed[17].

Many innovative technologies and management strategies have been developed in an attempt to reduce the leakiness of annual cropping systems; they include adjustment of the timing and frequency of fertilizer application, adjustment of planting dates, application of nitrification or urease inhibitors, and planting of cover crops[19,20]. While these efforts are extremely important, it is arguable that attempts to modify annual agriculture have reached a stage of diminishing returns—technological advances have resulted in improved recovery of applied N, but the costs of technology, skilled labor and management are likely to be much greater for N recovery levels higher than 50%.

In contrast to modern annual agroecosystems, most native ecosystems maintain high levels of nutrient synchrony, particularly for limiting nutrients. For example, as

Table 1. Examples of net primary production (NPP), biomass-nitrogen (-N) and leached-N from perennial native vegetation, annual crops and perennial crops from temperate regions.

Ecosystem	Location	NPP (dry biomass)	Plant biomass-N	Leached-N	Leached-N/ biomass-N	Sources
		---------- kg ha^{-1} yr^{-1} ----------			%	
Native systems						
Temperate deciduous forest	New Hampshire, USA	10,400	523	4	<1	21
Tallgrass prairie	Kansas, USA	4170[1]	140[2]	<1[2]	<1	22, 23
Annual agroecosystems						
Barley fertilized 120 kg yr^{-1}	South-central Sweden	9630	183	10	6	24, 25
Corn fertilized 187 kg yr^{-1}	Iowa, USA	20,000[3]	201[3]	60	60	26
Perennial agroecosystems						
Perennial fescue fertilized 200 kg yr^{-1}	South-central Sweden	14,640	380	1	<1	24, 25
Alfalfa	Minnesota, USA	11,315[1]	343[4]	2	<1	27

[1] Above-ground net primary production (ANPP) only.
[2] Median values for prairie watersheds with fire frequencies ranging from 1 to 20 years (includes roots and shoots).
[3] Estimated ANPP and biomass-N based on extrapolations from reported grain yield of 10 MT ha^{-1}.
[4] Plant biomass-N for above-ground biomass only.

a percentage of N contained in live plant biomass, native ecosystems commonly lose one to two orders of magnitude less N to leaching than do annual agroecosystems (Table 1)[21–27]. High retention of N and other essential nutrients in most native ecosystems is, in many respects, attributable to the predominance of perennial vegetation. Perennial plants retain nutrients in two important ways: (1) through retranslocation within plants before tissue senescence; and (2) by maintaining extensive root systems that can capture nutrients in broad windows of time and space. When multiple perennial species grow together, the efficiency of nutrient capture increases further. For example, native perennial grasses maintain different tissue qualities, root:shoot ratios and, in turn, nutrient mineralization rates[28]. Variation in these and other species-specific attributes leads to spatial and/or temporal partitioning of nutrient resources[29,30] and ultimately reduces the likelihood of large pools of available nutrients accumulating in soils and then being lost through leaching or denitrification.

Levels of nutrient synchrony that approach those of native systems have been achieved in perennial pasture and forage cropping systems[17]. In the Kjettslinge farm study in Sweden, researchers measured leaching outputs of only 1 kg N ha^{-1} yr^{-1} from a perennial fescue (*Festuca pratensis*) ley that received 200 kg N ha^{-1} yr^{-1} as fertilizer[24,25] (Table 1). In tile-drained plots in Minnesota, Randall and colleagues[27] reported that plots of alfalfa leached 37 times less nitrate than annual continuous corn or corn–soybean rotations. These findings and others[31–33] suggest that herbaceous perennials have the potential to maintain high NPP, biomass harvests and high levels of nutrient synchrony. With every kilogram of nutrient that is retained in a perennial cropping system, one less kilogram of nutrient input is required to support high yields.

Balancing Nutrient Losses with Endogenous Nutrient Inputs

It is widely accepted that plants require 14 elements other than oxygen, hydrogen and carbon, which they directly obtain from air and water[34]. These 14 elements or nutrients are N, P, K, Ca, Mg, S, Mn, B, Zn, Cu, Ni, Cl, Mo and Fe. Several other elements—Co, Na, Si—are essential to particular plants, or at least enhance their growth[34]. Of all the essential nutrients required by plants, only N originates almost entirely from the atmosphere and is 'fixed' or made available to the biota by organisms[35]. All other essential nutrients originate from the dissolution of primary and secondary minerals, or in other words, the weathering of rocks and soils. In this paper, I refer to these as 'lithophilic' (rock-loving) nutrients, to identify them as elements that cycle on a geological time scale. For a nutrient to be lithophilic does not imply that it was recently weathered from a rock mineral, simply that the origin of the nutrient can ultimately be traced back to the dissolution of rock minerals. In ecosystems with young to middle-aged soils, N is the nutrient that most commonly limits NPP of native and unfertilized agroecosystems[36]. In ecosystems developed on older, highly weathered soils, the low biotic availability of P or another lithophilic element often becomes the most limiting nutrient to productivity[37,38].

N limitation as a lithophilic nutrient limitation in disguise

The reasons why N limitation develops and persists in young to moderately developed ecosystems are complex and not entirely understood. Broadly speaking, there are numerous pathways for N loss to occur in most

ecosystems[36,39], and rates of loss through these pathways are imperfectly matched by rates of N inputs via atmospheric deposition and biological N fixation. In ecosystems where N limitation is chronic, one would expect organisms with the capacity to fix N to have a competitive advantage over organisms having to compete for limited soil N[36]. Occasionally this is what is found, but often in temperate regions, potentially competitive N fixing species, such as woody legumes, are absent from the flora of N-limited ecosystems[40]. Alternatively, when legumes are present in the flora, the activity of N fixers is frequently constrained by one or more of the following ecological factors: the energetic costs of fixing N, preferential herbivory of N-rich legumes, sensitivity of N fixers to fire, extreme soil pH, drought or low availability of lithophilic nutrients[35,36,41].

Many of the factors that prevent legumes from eliminating N-limitation in native systems are effectively addressed through management practices in legume-based agroecosystems (e.g., adjustment of legume density and spacing, rhizobial inoculation, irrigation, control measures for weed competition and herbivory). However, it is difficult to increase the availability of lithophilic nutrients that affect N fixers through farm management practices. The activities of symbiotic N-fixing bacteria can be affected directly or indirectly (*vis-à-vis* host vitality) by a range of lithophilic nutrients, including K, Ca and Mo[42–44]. However, the availability of P stands out as a nutrient that has been shown to affect N fixation rates of rhizobia in legumes[43,45–49], as well as free-living bacteria, both heterotrophic[50] and autotrophic[51].

The requirement for key lithophilic nutrients by N-fixing symbioses led Vitousek and Howarth[36] to suggest that N limitation in some ecosystems is actually 'limitation by some other nutrient in disguise'. Certainly, in agroecosystems where legume densities can be adjusted, N availability might be best characterized as a proximate limiting factor, with the availability of lithophilic nutrients required by N fixers being an ultimate limiting factor. Crews[52] illustrated this in research on a traditional farming system that is found in different physiographic regions of south-central Mexico. Farmers grew maize and alfalfa—the alfalfa was fed to livestock whose manure was used to fertilize the maize. N fixation by alfalfa, and thus N supplies to the maize via manure, was regulated in part by the availability of native soil P.

Weathering rates of essential lithophilic nutrients

An adequate supply of lithophilic nutrients is essential for crop growth and for N fixation. As with N, farmers have increasingly addressed crop limitations caused by inadequate supplies of lithophilic nutrients by applying mineral fertilizers. Also as with N, the prospect of improving the synchrony of crop demand with nutrient supply could substantially decrease the need to use exogenous nutrients to balance losses. But the question remains, is it possible for soils alone to continuously supply adequate levels of lithophilic nutrients to crops, especially when they are being removed continuously in harvests? The experience of most annual agriculture suggests that the answer to this question is no, at least not when yields are great[8]. However, if nutrient synchrony can be substantially increased with perennials, then continuous production based solely on endogenous nutrient supplies may be possible on some soils in certain climates (Fig. 2). To understand where these soils might be found, I will describe three soil-related attributes that broadly determine rates of lithophilic nutrient release from weathering; namely, original parent material structure and composition, stage of soil development and current climate.

Original parent material structure and composition

Soil parent material refers to the original rock or deposited material (alluvial, colluvial, eolian) from which a soil develops. Rock-forming magmas in the Earth's mantle vary considerably in their lithophilic nutrient concentrations, and these variations are reflected in the constituent minerals that comprise rocks at the Earth's surface[53]. Moreover, variation in cooling and depositional processes can affect nutrient concentrations of rocks and minerals. For example, the P concentration of the constituent minerals of a typical granite is 0.05%, compared to a typical basalt, which is 0.15%[54].

Equally important as the lithophilic nutrient content of rock and mineral parent materials is their stability under Earth surface conditions. Geomorphologists utilize numerous elemental ratios to evaluate the susceptibility of different geological substrates to weathering reactions[55]. Reiche's weathering potential index (WPI)[56] relates the mole percentage of the sum of alkalis and alkaline earth elements (the most mobile ions in the weathering process) minus combined water (an indication of the extent of hydrolysis already taken place) to the total moles present in the mineral exclusive of water (see Eqn 1).

Reiche's WPI is intended to reflect: (1) the stability of the crystalline structure of a mineral; and (2) the extent to which a mineral has already been weathered[56,57]. Substrates with high WPI values are considered less stable and thus more weatherable (Table 2). While very qualitative, the WPI values, coupled with lithophilic nutrient concentrations, illustrate which parent materials have the propensity to weather relatively quickly and, in the process, release essential nutrients.

Stage of soil development and lithophilic nutrient availability

In the past several decades, biogeochemical theory has developed suggesting that nutrient availability of a soil is not simply a unique property reflecting complex local circumstances but, rather, is understandable within a broad framework of biogeochemical changes that occur during long-term soil development[37,39,58]. For example, Walker

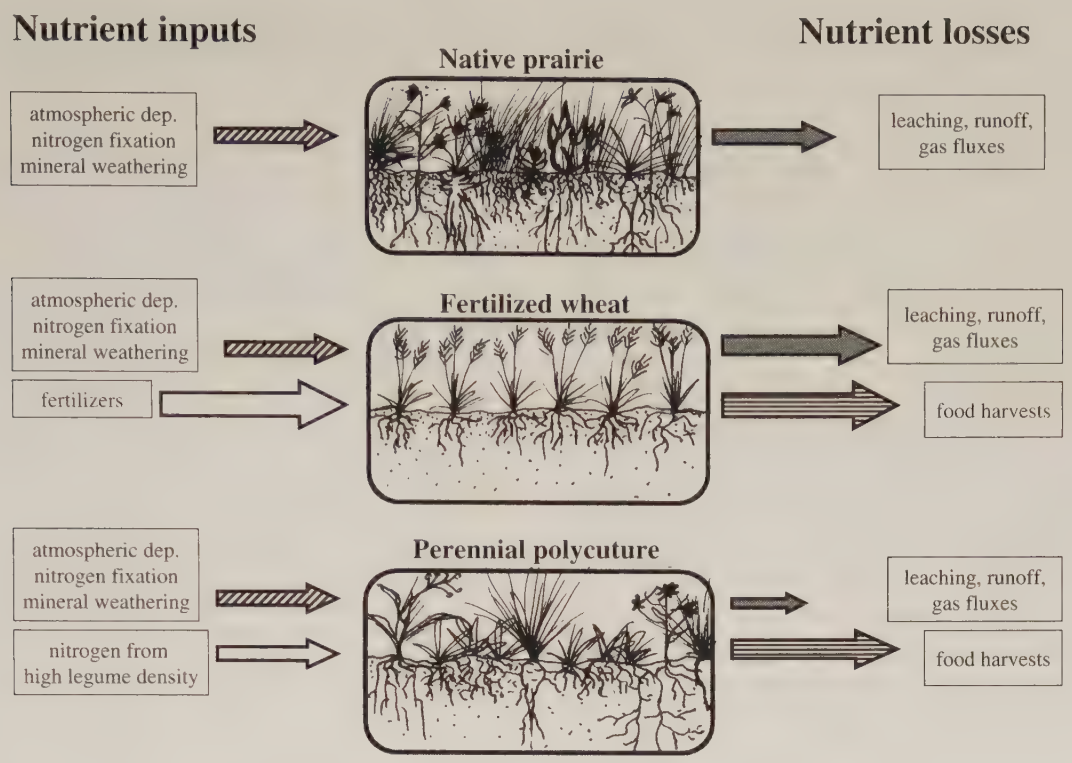

Figure 2. Relative avenues of nutrient inputs and losses for native prairie, annual wheat and a perennial polyculture; dep.; deposition.

$$\frac{100\times\text{moles}(K_2O + Na_2O + CaO + MgO - H_2O)}{\text{moles}\ (SiO_2 + TiO_2 + Al_2O_3 + Fe_2O_3 + Cr_2O_3 + K_2O + Na_2O + CaO + MgO - H_2O)}. \quad (1)$$

and Syers[37] proposed a model of how forms of soil P change over the course of long-term soil development (Fig. 3). They suggested that at the onset of primary succession, when a new parent material is exposed for colonization by the biota, all P is held in primary minerals, the most common being apatites (P_{Ca}; calcium phosphates containing varying quantities of carbonate, fluoride, sulfate, hydroxide and several cations). Since apatites are generally contained in rocks or large particles of primary minerals, P availability at very early stages of soil development tends to be low. Through the action of weathering, the primary mineral-P dissolves, and the labile phosphate is either taken

Table 2. Examples of calculated weathering potential index (WPI) values[56] and percentages of calcium (%Ca) and phosphorus (%P) for selected parent materials[54].

Rock type	WPI	%Ca	%P
Rhyolite	2.5	0.81	0.03
Granite	7	1.31	0.05
Gneiss	7	0.09	0.04
Schist	7	0.81	0.04
Diorite	13	4.67	0.13
Andesite	14	4.82	0.09
Basalt	18	6.72	0.15
Gabbro	22	6.80	0.11

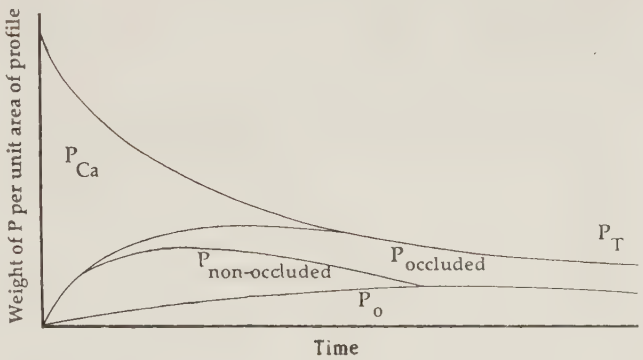

Figure 3. Walker and Syers' model[37] of changes in forms of soil phosphorus thorough time. P_T = total soil P, P_{Ca} = primary mineral calcium phosphates (largely apatite minerals), P_o = organically bound P, $P_{non\text{-}occluded}$ = relatively labile P that could potentially be available to the biota, $P_{occluded}$ = sparingly soluble P, largely associated with oxides of Fe and Al and mostly unavailable to the biota.

up by organisms, thus entering the organic P pool (P_o), or sorbed onto charged sites of secondary minerals—especially hydrated forms of Fe or Al oxides (referred to as the non-occluded P_i pool).

At some intermediate stages of soil development, Walker and Syers[37] predicted that biologically available P would be greatest, as much of the P_o and P_i fractions are relatively labile. As soils develop further, silicate clay minerals give way to dominance by Fe and Al hydrous oxides, and P associated with these minerals becomes increasingly occluded and unavailable. In addition, the soil organic matter pools become increasingly recalcitrant, rendering P in the P_o pool less biologically active as well. Soils of temperate regions do not generally reach this later stage of soil development, as glaciation has periodically reset the clock of soil development to initial stages. The Ultisols and Oxisols of the tropics, on the other hand, are representative of highly weathered soils dominated by Al and Fe secondary minerals.

The model of Walker and Syers[37] was tested on a soil age-gradient spanning early to late stages of soil development under native rainforest across the Hawaiian archipelago[59]. While there were some interesting differences between Walker and Syers' model and results from the Hawaiian archipelago, overall, P changes across the Hawaiian chronosequence agreed to a large extent with model predictions (Fig. 3). In Hawaii, primary mineral P declined in the first 20,000 years of soil development, causing an increase in non-occluded P and P_o. In later stages of ecosystem development non-occluded P_i and P_o decreased as percentages of total P, and occluded P increased. The testing of the Walker and Syers' model is relevant to sustainable agriculture because current nutrient availability in Hawaii was found to be directly related to long-term changes in soil biogeochemistry[39,59,60]. Soil available P on the Hawaii soil age-gradient increased in the first 20,000 years of soil development, and then began to fall, as primary apatite minerals became exhausted (Fig. 4a). The availability of base-forming cations exhibited similar trends (Fig. 4b)[39].

As discussed above, the original parent material of a soil can have an important influence on its ability to supply lithophilic nutrients to the biota. Equally important is where a parent material and soil are in the context of long-term development. The findings from the Hawaiian study suggest that there is a high lithophilic nutrient release stage of soil development (Fig. 4a,b). Lithophilic nutrients from weathering are substantially exceeding biological uptake during this stage. In a native ecosystem this nutrient excess exits the ecosystem through leaching and into rivers, but in an agroecosystem with high nutrient retention, it could sustain food harvest exports (Fig. 2). This stage is likely to begin when sufficient primary minerals have broken down or undergone dissolution to release lithophilic nutrients which are essential to the growth of vegetation as well as the activities of symbiotic or asymbiotic bacteria[50,58]. The stage appears to end when most primary minerals in the rooting zone have been exhausted through weathering, and the soils become acidic, with low cation exchange capacity.

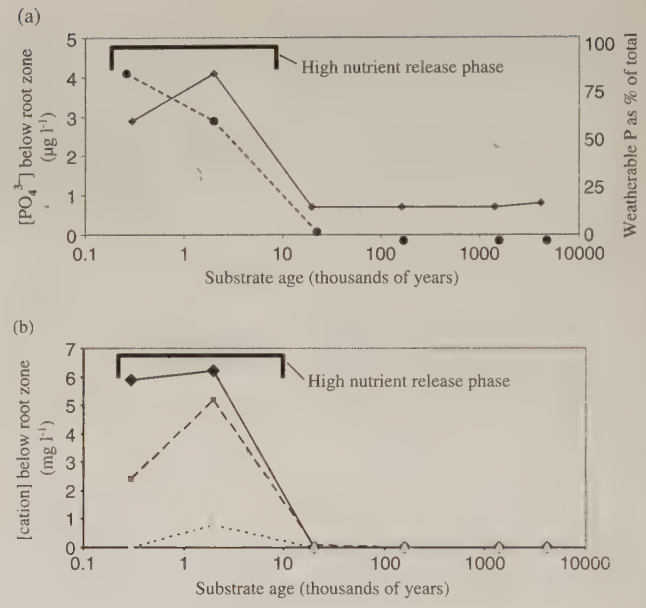
(a)
High nutrient release phase
[PO_4^{3-}] below root zone (μg l⁻¹)
Weatherable P as % of total
Substrate age (thousands of years)
(b)
High nutrient release phase
[cation] below root zone (mg l⁻¹)
Substrate age (thousands of years)

Figure 4. Changes in lithophilic nutrients with soil development across a 4.1 million year chronosequence in Hawaii: (a) Changes in % weatherable phosphorus (P) from primary minerals (dashed line) and concentrations of labile P below the rooting zone (solid line); (b) changes in concentrations of labile base cation nutrients below the rooting zone: Ca^{2+} (solid line), Mg^{2+} (long dash), K^+ (short dash). Note log scale on *y*-axis. (Modified from Hedin and colleagues[39].)

Crews[61] characterized the forms of soil P in soils sampled from numerous never-fertilized traditional farms in south-central Mexico that had been cultivated continuously for a minimum of 200 years. All soils contained ratios of primary mineral P to total P between 0.08 and 0.57[61] (Fig. 5). All of these soils fall within the high lithophilic nutrient release phase described in the Hawaiian study (Figs. 4a,b). Other researchers have found that the cultivation of previously unplowed soils often results in substantial net mineralization of organic P, which can support crop requirements for 10–100 years[62,63]. However, in much older agroecosystems, average net ecosystem production should approach zero, at which time P is sequestered in newly formed organic matter as fast as it is mineralized. Thus Crews[61] concluded that for older, unfertilized and continuously cultivated agroecosystems to be viable, net P exports in harvests must be made up by dissolution of primary P-bearing minerals.

Current climate

The timing and duration of a particular soil's nutrient release stage will vary depending, to a large extent, on parent material and climate. The stage occurred fairly quickly in the Hawaiian soil age-gradient (when depicted on a non-log scale) because the basalt parent material has a

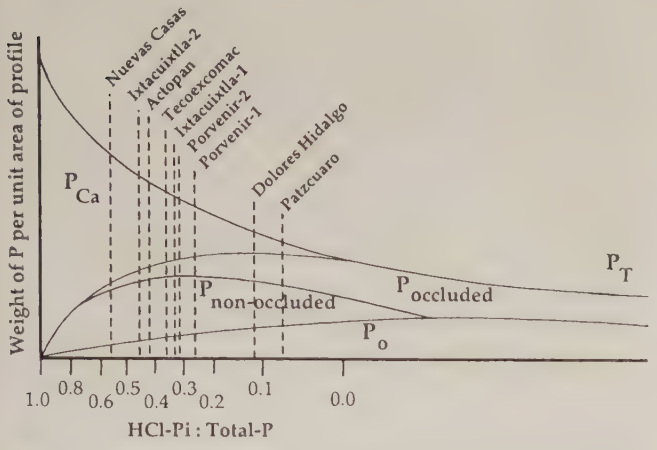

Figure 5. Placement of continuously productive traditional farming sites in Mexico on the Walker and Syers'[37] model of changes in soil phosphorus (P) forms with time. Soils were sampled from 3-year-old alfalfa stands and sites were situated on the model using HCl-Pi (P_{ca}):P_T (primary mineral P to total P) ratios. Farms were reported to have been in production for >200 years[61].

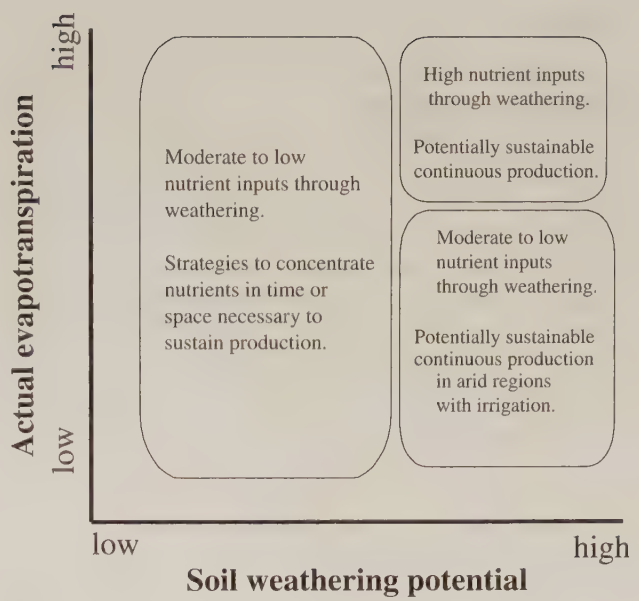
Actual evapotranspiration
high
low
Moderate to low nutrient inputs through weathering.
Strategies to concentrate nutrients in time or space necessary to sustain production.
High nutrient inputs through weathering.
Potentially sustainable continuous production.
Moderate to low nutrient inputs through weathering.
Potentially sustainable continuous production in arid regions with irrigation.
low
high
Soil weathering potential

Figure 6. A conceptual model showing where high rates of lithophilic nutrient release might sustain an agroecosystem with high synchrony. Potential nutrient release is presented as a function of weathering potential of soil and rock minerals and the combined influence of temperature and precipitation (actual evapotranspiration).

high weathering potential (Table 2), and the climate is favorable for weathering reactions, with a mean annual temperature of 16°C and annual precipitation of 2500 mm. More moderate levels of nutrient release are likely in ecosystems where the climate is either drier or colder, or the parent materials have a lower WPI.

Figure 6 depicts a simple conceptual model that combines substrate WPI (soil + parent material) and climate (actual evapotranspiration or AET) to indicate where nutrient release might be sufficient to balance harvest losses in a perennial polyculture. Actual evapotranspiration (AET) is a measure of transpired and evaporated water loss from an ecosystem. It is a useful surrogate for the simultaneous availability of water and solar energy in an environment during a defined period of time[64]. Several authors have suggested the utility of using AET to predict mineral weathering rates[65,66]. In addition to the direct effects of AET on mineral dissolution, temperature and precipitation are also primary drivers of the biological processes associated with NPP and decomposition which have been shown to affect mineral weathering rates profoundly[64,67–69].

Empirical studies that have attempted to estimate actual lithophilic nutrient release through weathering have proven challenging, particularly for P, due to our inability to distinguish between newly weathered P (an input) and P that has been mineralized from organic matter (cycling P). In an impressive review of the subject, Newman[70] found direct estimates of P release by weathering to range between 0.05 and 1.0 kg P ha^{-1} yr^{-1}; however, these estimates largely came from soils that were significantly weathered and not likely to have high apatite contents. Using indirect evidence (Si dissolution measurements), Newman[70] estimated that P dissolution rates of 5 kg ha^{-1} yr^{-1} were possible. This indirect estimate could sustain harvest exports of 1500 kg wheat grain ha^{-1} yr^{-1}[18]. While Newman considered 5 kg ha^{-1} yr^{-1} to be at the high end of probable P weathering rates, there has simply not been enough work to constrain this value accurately. Variation in parent material, rooting depths and rhizosphere effects are tremendous[53,68,71,72] and little understood in terms of quantitative effects on weathering rates. That said, there clearly exist upper limits to lithophilic weathering rates. To increase agricultural production beyond what the upper limit will allow, it would be necessary for farmers to employ a strategy of concentrating nutrients in time or space, to recycle nutrients in human manure back into agroecosystems, or to apply exogenous fertilizers.

Optimizing legume density, harvest and disturbance regimes

Of all the essential nutrients, N limitation should be the easiest to address, given our ability to overcome N deficits through biological N fixation. However, using legumes to meet the N requirements of a perennial polyculture will involve considerable attention to crop species selection, breeding and cropping systems design. Moreover, numerous management strategies must be considered to maximize the transfer of N fixed by legumes to non-fixing crops[17,18]. Here I will describe three important aspects of legume-based polycultures that will require optimization to sustain appreciable yields: they are the legume harvest index, cropping density and %N derived from the atmosphere.

Legume harvest index

The legume component of the perennial polyculture assemblage has potential as a source of protein-rich food for human or livestock consumption. However, this role of the legume as a food crop may conflict with its role as N supplier to the other members of the perennial polyculture. As with many plants, seed production in legumes constitutes a substantial N sink, and if this sink requires too much of the total N fixed by the legume, it will fail to supply adequate N for non-fixing species of the polyculture. The net N contribution of a legume crop to the agroecosystem can be determined using equations 2–4[73].

$$N_{contribution} = Nf - Nls \quad (2)$$

$$Nf = (P_{fix} \times Nl) \quad (3)$$

$$Nls = (NHI \times Nl) \quad (4)$$

where: $N_{contribution}$ = net legume N contribution to the polyculture;
Nf = N in legume from N fixation;
Nls = the amount of total legume N allocated to seed;
P_{fix} = proportion of N in legume from N fixation;
Nl = total N in legume; and
NHI = N harvest index—the proportion of N allocated to seed.

The extent to which legume N is allocated to non-legumes in the cropping system versus a seed crop is mainly a function of the legume's N harvest index (NHI)—that is, the percentage of the total plant N that is allocated to the seed—and the proportion of N in the legume that originated from fixation versus soil recovery (P_{fix}). Simply put, for the polyculture legume to make a net N contribution to other non-fixing members of the community, P_{fix} must be greater than NHI[73]. The greater P_{fix} is relative to NHI, the more N will be available to non-fixers. Obviously, if no seed N is harvested, then all of the N that is fixed in the legume will become available to the biota. Recent improvements in estimating below-ground N contributions by legume species have effectively increased estimates of total legume N (Nl), often by about 40%[74,75]. Given these revised total N budgets, it appears more possible than previously thought that the legume component of a polyculture could be managed to simultaneously produce a crop and maintain soil N fertility.

Legume cropping density

In order to meet the N requirements of the non-legume crop species, the density or % cover of legume in the polyculture will have to be optimized (Fig. 7). Essentially, the N contribution of the legume from N fixation has to equal, on a mass balance, the sum of N losses from the agroecosystem, which includes all grain harvests (including any harvested legume seed), as well as N that escapes via denitrification, ammonia volatilization, runoff and leaching (Eqns 5 and 6).

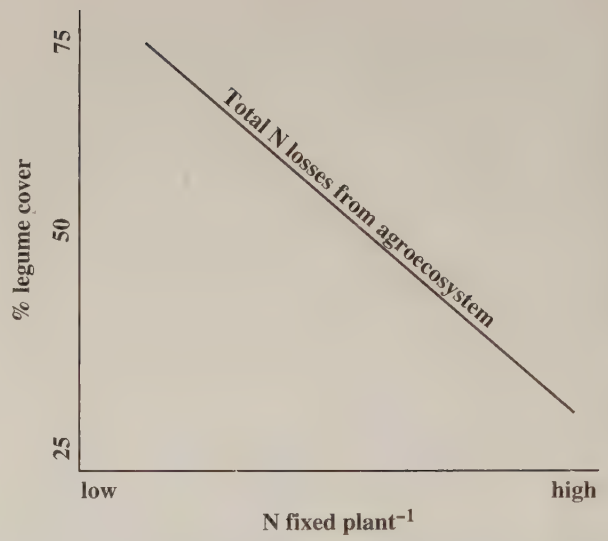

Figure 7. The relationship between nitrogen (N) fixed per legume plant and the % cover of legumes needed in a perennial cropping system to balance N losses. The N loss curve represents one set rate of N losses from the agroecosystem in harvests, denitrification, ammonia volatilization, leaching and runoff.

$$L_{density} = N_{losses}/N_{f\text{-}plant}/1000 \quad (5)$$

$$N_{losses} = NLC_{harvest} + Nls + N_{escape} \quad (6)$$

where: $L_{density}$ = legume plants ha^{-1} required to balance N losses from the agroecosystem;
$N_{f\text{-}plant}$ = N fixed per legume plant (g yr^{-1});
$NLC_{harvest}$ = N in non-legume crop (kg ha^{-1} yr^{-1});
Nls = N in legume seed (kg ha^{-1} yr^{-1}); and
N_{escape} = total N that escapes from the agroecosystem via ammonia volatilization, denitrification, leaching and runoff (kg ha^{-1} yr^{-1}).

It is possible that a polyculture of perennial plants with diverse N acquisition strategies might self-optimize legume density in response to polyculture N demands. Ledgard[76] reported findings from a non-fertilized pasture where, over 5 years, clover densities and contributions from N fixation varied as a function of soil N availability, climate and pest/disease cycles (Fig. 8a,b).

Percent N derived from the atmosphere (%Ndfa)

As illustrated in Equation 3, the proportion, or percentage, of N that a legume acquires from the atmosphere through N fixation (P_{fix}) is a critical variable in determining whether legumes that are harvested for food can also make a net contribution to the N economy of other crops. When multiplied by 100, P_{fix} can be converted to the term '%N derived from the atmosphere', or %Ndfa, which can vary substantially from 0 to 98%[77]. In considering the N-supplying role of the legume in a perennial polyculture, it is critical to explore ecosystem dynamics that maintain high %Ndfa values, regardless of whether the legume is eventually harvested for grain. Soil N availability is a

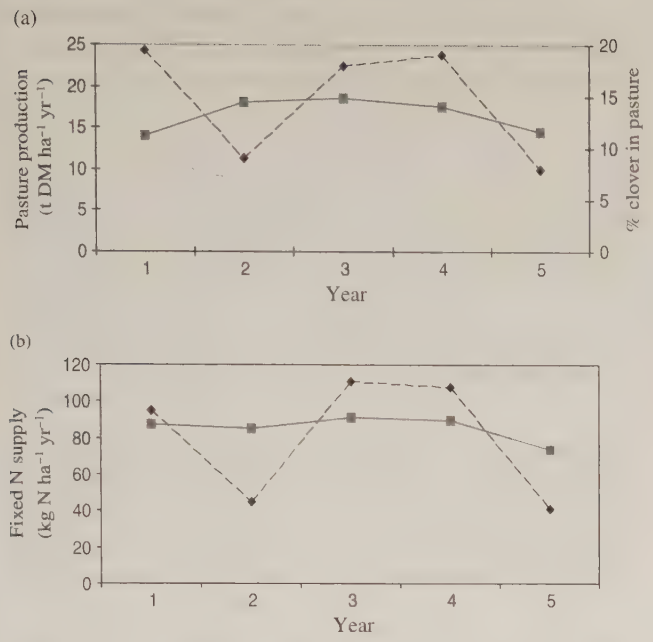

Figure 8. Relationships between legume and grass abundance in a pasture community as a function of N fixation and soil N availability over a 5-year study: (a) annual changes in total pasture production (solid line) and % clover cover (dashed line); (b) clover fixed N supply (dashed line) and modeled estimates of annual N availability from legume residues (solid line). (From Ledgard[76].)

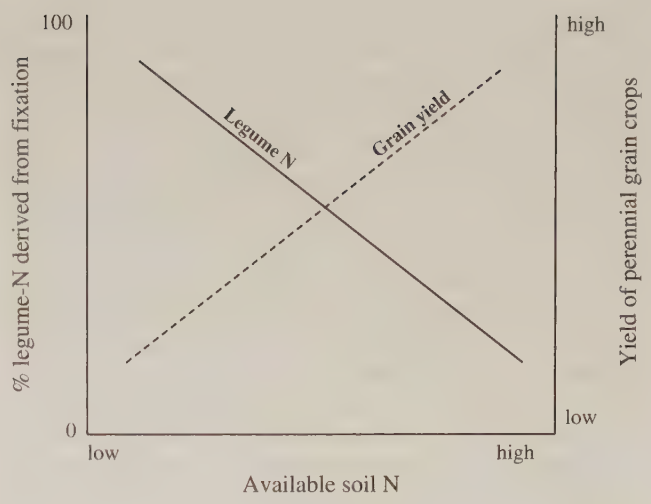

Figure 9. Potential trade-offs in a perennial polyculture between legume N-fixing efficiency (%Ndfa) and potential grain yield, resulting from shifting supplies of available soil N.

major determinant of N fixation by legumes[35,73,76]. The metabolic costs of taking up NH_4^+ or NO_3^- from the soil typically requires less plant energy than N fixation, at least when nitrate reduction is carried out in leaves[34,35].

There may exist a tension between the simultaneous requirements of maintaining high rates of N supply to maximize grain yields, and maintaining high %Ndfa in the legume crop to supply future crops with N (Fig. 9). Traditional farmers who relied on legumes to supply grain crops with N generally avoided this tension by separating the N-fixing legumes from the crop in time or space. For example, in a traditional Mexican agroecosystem, monocropped plots of alfalfa were intensively harvested to supply forage to animals and ultimately manure to maize plots; in this way, plant available N was minimized in the rhizosphere of the N fixer, and maintained at a high level in the rooting zone of the grain crop.

As with the optimization of legume cover in the pasture community described by Ledgard[76] (Fig. 8a,b), it is possible that the %Ndfa of legumes will, to some extent, self-optimize in relation to the diverse spatial and temporal N uptake patterns of a polyculture. That said, there are numerous avenues of research that could potentially increase the %Ndfa of perennial legumes grown in polyculture.

Selection or breeding for nitrate tolerance. The extent to which nitrate negatively affects rates of N fixation varies considerably from species to species. Harper and Gibson[78] found the threshold concentrations of NO_3^- for complete suppression of N fixation to range from 2 to 20 m*M* (about 10.5–105 mg nitrate-N kg^{-1} soil). These findings suggest that legumes might be bred or selected to fix in the face of relatively high nitrate concentrations[79,80]. However, Ledgard[76] warns that breeding for nitrate tolerance could force the legumes in a mixed stand to be out-competed, due to the greater energetic costs incurred by the N fixers.

Breeding for the ability to switch rapidly between fixing N_2 and taking up soil N. In theory, legume competitiveness with grasses might be increased if legumes were able to respond to short-term changes in soil N status by quickly shifting their C allocation patterns between N fixation and growth[76].

Favoring the uptake of ammonium over nitrate. While ammonium has been shown to reduce N fixation in numerous actinorrhizal species[81], and many researchers acknowledge a negative effect of NH_4^+ on legume N fixation[34], its effect is not nearly as well documented as that of nitrate. Some researches have actually found legumes either to have no response, or a positive response, to the presence of ammonium in soils[82,83]. Gutschick[84] reported that N is taken up by plants in some grasslands at a sufficient rate to out-compete nitrifying bacteria. If little NO_3^- is allowed to accumulate, and NO_3^- is the form of soil-N responsible for inhibiting N fixation, then it is possible that fixers in these ecosystems will continue to fix even when substantial combined N (in the form of NH_4^+) is mineralized through the growing season[40]. Mycorrhizal fungal symbioses in the grass and sunflower components of the polyculture may play a key role in scavenging ammonium (or even forms of organic N) from the legume rhizosphere[85]. Like selecting or breeding for nitrate tolerance, this approach could result in non-fixers outcompeting legumes.

Selectively cutting the legume to cause concurrent N release. Selectively cutting the legume in the polyculture might function to induce root and nodule senescence and N

release. If a cutting were timed according to the uptake requirements of the non-fixing crops, mineralized N from the legume roots would be scavenged and greater legume N fixation would eventually be promoted. Alternatively, if the grass components of the perennial polyculture are shown to exhibit some degree of compensatory growth[86,87], then mowing or grazing the entire polyculture at an early or middle stage of the growing season may stimulate both N transfer and greater grass productivity.

Temporal separation of N fixation and high grain yields. A temporal separation of N fixation and the grain-producing stage of the cropping cycle might involve a 2-year rotation of grazing and harvesting—in the harvest year, the polyculture takes advantage of high soil N availability from the previous fallow year. During the grazing year, N fixers have a high P_{fix} because harvests in the previous year have drawn soil N levels down.

Spatial separation of legume and grass roots. Deep tap roots are common to prairie legumes. To the extent that N is transferred from the legume to non-fixing associated species via decomposing shoot residues, it is possible that the legume roots may occupy a zone of the soil profile that is relatively low in combined N compared to the surface horizons which are commonly more exploited by grass species.

Conclusion

Smil[88] has estimated that over 40% of humans alive today owe their existence to the Haber–Bosch industrial process of synthesizing ammonia. However, this estimate is based on an agriculture that leaks between 40 and 70% of applied N. If 40% more N was taken up by crops, then much less N would need to be fixed to achieve the same level of crop productivity. In other words, Smil's estimation of humanity's dependence on synthetic N might be accurate for annual agriculture, but if farming systems with greatly improved synchrony were developed, then the human dependence on industrial N sources would be reduced accordingly.

The development of perennial polycultures comprises one promising approach to improving N synchrony while maintaining relatively high yields. Increasing synchrony is an extremely important goal regardless of whether nutrient inputs originate from fertilizers or endogenous sources. However, synthetic fertilizers are ultimately not sustainable in the long term, as they are extremely energy intensive to produce, in the case of N, or finite and non-renewable, in the case of P and other lithophilic nutrients. If agroecosystems can be designed to maintain high rates of productivity while relying to the greatest extent possible on endogenous nutrient supplies, then the environmental impacts caused by excessive nutrient enrichment of the biosphere, as well as human dependence on non-renewable resources, will be lessened.

In this paper I have framed what I believe to be the most important considerations and challenges facing the initial development of grain-producing perennial polycultures with regard to endogenous nutrient acquisition. Some of the issues I raise may be resolved through currently unpredictable dynamics of interacting perennial functional groups (N fixer, warm-season grass, cool-season grass). However, there exist differences between the native prairie and a perennial polyculture, not the least of which is the likelihood of annual nutrient removal in harvests (Fig. 2). These losses could be matched, or at least greatly offset, by nutrient inputs from the weathering of soils that are in a high nutrient release phase of soil development, and through management of legume N fixation.

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A comparison of conventional and alternative agroecosystems using alfalfa (*Medicago sativa*) and winter wheat (*Triticum aestivum*)

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Abstract

Natural systems agriculture is based on an understanding that natural systems are self-sustaining due to regulatory mechanisms and processes that help to ensure the long-term maintenance of the ecosystem. An agroecosystem modeled after nature should encompass greater stability and biodiversity at all levels of organization than an agroecosystem based on conventional agricultural practices. The main objective of this study was to determine whether agroecosystems modeled after nature exhibit advantages over conventional agroecosystems. Five treatments were examined: winter wheat (*Triticum aestivum* L.) monoculture, alfalfa (*Medicago sativa* L.) monoculture, strip-cropped alfalfa and wheat, and two alfalfa–wheat intercrops (one no-till and one conservation-till). Indicators of ecosystem function studied included primary productivity, soil fertility, plant nitrogen (N) concentration, and abundances of arthropod pests and predators. No fertilizers or pesticides were used prior to or during this investigation. Monoculture, strip-crop and conservation-till treatments produced significantly higher yields than no-till intercropped alfalfa and wheat. Although yields from the no-till intercrop were low, wheat protein values were comparable to other treatments. Soil N concentrations tended to be high in treatments containing alfalfa. Insect pests preferred alfalfa and were, therefore, often more abundant in treatments containing high percentages of alfalfa, as were predators such as spiders. Researching alternatives to monoculture agroecosystems, such as the intercrop systems in this study, may provide us insight into a true natural systems agriculture.

Key words: agroecosystem ecology, alternative agriculture, *Medicago sativa*, natural systems agriculture (NSA), the Land Institute, *Triticum aestivum*

Introduction

Modern agriculture encourages increased production and yield maximization without examining long-term consequences, such as soil degradation, pesticide contamination of groundwater and declining biotic diversity[1]. Although a new model of the agricultural system is needed, current infrastructure is not equipped to handle this monumental change. Therefore, smaller steps must be taken now to move modern agricultural practices away from increased subsidies (pesticides, fossil fuels and fertilizers) and toward sustainability based on naturally occurring ecological processes[2].

If we incorporate basic ecosystem concepts, such as those in naturally occurring ecosystems (e.g., niche differentiation, use of keystone species and nutrient cycling) into management programs, then we may be able to design agroecosystems that are more self-sustaining and depend less on external energy inputs[3]. Diversity of species and function is a major component of, and regulatory mechanism in, natural grassland ecosystems[1]. These two types of diversity can be integrated into cropping systems by simultaneously cultivating more than one crop species in a field and by using crop species from different functional groups. The four main plant guilds in grassland ecosystems are perennial C_3 grasses, perennial C_4 grasses, nitrogen fixers and composites[1].

Another feature of natural grassland ecosystems is minimal soil disturbance (i.e., no mechanical tillage) compared to conventional agriculture, which has traditionally relied on tillage. By examining the effects of incorporating greater crop diversity and decreased tillage into agricultural systems, we can compare the relative advantages and disadvantages of alternative agroecosystems that incorporate

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the features of natural grasslands with more conventional agroecosystems.

Plant interactions

Increased biotic diversity provides benefits for plant communities, including higher rates of primary production per unit area of land[4]. A proposed mechanism for this increased productivity is higher soil resource-use efficiency in diverse stands compared to monocultures[5]. Plants from different functional groups require large amounts of nutrients at different times during the growing season[4], and different functional groups use different resources, resulting in niche differentiation[5].

We selected perennial alfalfa (*Medicago sativa*) and annual winter wheat (*Triticum aestivum*) to establish our cropping treatments. Because root morphologies and physiologies of alfalfa and wheat are quite different (i.e., they do not compete for the same resources), total uptake of water and nutrients may be improved when both species are grown together. Perennial alfalfa has a long tap root that is efficient for obtaining water and nitrate at greater depths than fibrous wheat roots[6]. Therefore, alfalfa may obtain water and nutrients that are leached below wheat roots, increasing total resource uptake. Complementary use of resources may result in a condition termed overyielding. Overyielding occurs when two species grown together are more productive per unit area than would be expected based on monoculture yields[7].

Facilitation is another mechanism that may result in increased net primary production in an intercrop, whereby the presence of one species enhances the growth of another species[7,8]. One mechanism contributing to facilitation in a legume–grass intercrop is the legume's input of nitrogen (N) into the soil. Because legumes compete poorly with grasses for mineral soil N[9], they can be used as companion species for intercropping with grasses (i.e., legumes are able to fix atmospheric N when adequate soil N is not available).

We investigated the contribution of intercropped alfalfa to soil and wheat-grain nitrogen concentrations. Yields of intercropped and monoculture wheat and alfalfa were also quantified to determine whether overyielding occurred in any of the intercropped systems.

Arthropods

We also sought to determine how ecosystem biotic diversity is related to different management practices. Focus has recently turned to cultural methods to control pests, because pesticides frequently have adverse impacts on ecosystem function, including the elimination of beneficial insects[10]. Cultural control of pests in agroecosystems includes designing cropping systems to avoid pest outbreaks. One form of cultural control is intercropping, or increasing the diversity of crop species[11].

Insect pest damage has been shown to be more harmful in monocultures than in diverse stands of vegetation[12,13]. Root[14] proposed the 'resource concentration' hypothesis as a possible explanation for higher numbers of arthropod pests in monocultures. He suggested that specialist herbivores whose requirements are fulfilled by plants in a less diverse environment tend to remain and reproduce in that environment. Specialist herbivores often rely on chemical and visual cues from their host plants to feed and reproduce[15]. Findings suggest that chemical signals from non-host plants interfere with the ability of herbivores to find suitable food and reproduce[16,17].

Multicropped agroecosystems may also attract more generalist predators and parasitoids, which could potentially control herbivore populations. Root[14] formulated the 'enemies' hypothesis as another possible explanation for lower pest numbers in heterogeneous agroecosystems. This hypothesis suggests that predators are more likely to remain in heterogeneous systems due to diversity of food resources and refugia. Although the enemies hypothesis has received less support than the resource concentration hypothesis, it continues to be researched as an important mechanism of pest control[18]. Our investigation sought to determine whether agricultural systems involving more than one crop species exhibited advantages over conventional monoculture systems.

Materials and Methods

This investigation was conducted during the growing season (April–September) in 2001 and 2002. The field site was located at the Land Institute in Saline County, Kansas (97°36′W, 38°46′N). Prior to this experiment, the field site had been in continuous alfalfa (variety Cimmaron VR) cultivation since 1996. Soil type was Hord silt loam (fine-silty, mixed, mesic Cumulic Haplustoll) (Soil Survey of Saline Co., Kansas). Average annual rainfall is approximately 76 cm, with 47 cm occurring from April through August. Only 31 cm of rain fell from April through August 2002, resulting in a drought that severely reduced wheat production.

Plots were established in a randomized block design consisting of 3 blocks and 5 treatments. Treatments were: wheat monoculture (conventional till), alfalfa–wheat strip crop (wheat strips till; alfalfa strips no-till), alfalfa–wheat row intercrop (no-till), alfalfa–wheat row intercrop (conservation-till), and alfalfa monoculture (no-till). Strips in the strip-crop treatment were 3.64 m (12 feet) wide. Both strip-crops and row intercrops can be considered more ecologically complex systems than traditional monocultures. Planting two crop species in close proximity may have effects on faunal diversity, soil nutrient dynamics and resource use.

Conservation tillage in the conservation-till alfalfa–wheat intercrops entailed coarsely disking the surface soil once prior to wheat seeding. No-till alfalfa–wheat intercrops were planted using a no-till drill to seed wheat into the alfalfa stand. The seeding rate of crop species was the same for each treatment. Each plot (45 m × 45 m) was

separated from other plots by a 1 m buffer of alfalfa. No fertilizers or pesticides were applied to any of the plots prior to or during the experiment. Weed species found included foxtail (*Setaria viridis*, *S. glauca*), Japanese brome (*Bromus japonicus*), cheat grass (*B. tectorum*) and prickly lettuce (*Lactuca seriola*).

Agroecosystem parameters quantified included crop yields, grain and soil nitrogen, and arthropod pest and predator abundances. One-way analyses of variance were used when possible (SAS version 8.2, SAS Institute software, Cary, North Carolina, USA). Means were separated by pairwise comparisons (Fisher's protected least significant difference).

Estimating yield

Mean yield values during 2001 and 2002 were estimated from three random 0.75 m × 0.75 m samples per harvest period. For the first alfalfa harvest in each season, alfalfa was harvested in alfalfa monocultures and alfalfa strips within the strip-cropped bicultures. For the second harvest each season, alfalfa and wheat straw were clipped simultaneously in all treatments. All vegetation was dried at 60°C to constant mass.

To measure weed biomass, weeds were separated by hand from alfalfa and wheat samples. Although alfalfa in the wheat monoculture and wheat strips could be considered a weed, we kept alfalfa biomass separate from all other weed species. After 2 years of full tillage, alfalfa no longer grew in the wheat monoculture and wheat strips; therefore, no alfalfa was present in wheat strips or wheat monocultures in 2002.

Wheat was harvested with a combine in 2001 to estimate wheat grain yield. One strip running the length of each replicate plot was harvested with the head of the combine set just above the top of the alfalfa plants. In 2002, wheat growth was stunted due to drought conditions; thus the alfalfa in both the no-till row intercrop and in the conservation-till row intercrop was taller than both wheat varieties during the entire growing season. Therefore, three 0.75 m × 0.75 m samples per wheat variety were harvested in 2002 by hand rather than with a combine. Grain was cleaned following harvest, dried to constant mass and weighed to the nearest gram.

Mean yield values per treatment, including wheat, alfalfa and weeds, were compared using one-way ANOVAs. Relative yields were also analyzed using the land equivalent ratio (LER)[19]. LER values are a measure of land-use efficiency of intercrops; efficiency refers to harvestable biomass per unit land area. The formula is as follows:

$$\mathrm{LER} = \mathrm{RY_w} + \mathrm{RY_a},$$

where $\mathrm{RY_w}$ is the relative wheat yield and $\mathrm{RY_a}$ is the relative alfalfa yield.

Relative yields are obtained by comparing intercrop yields to monoculture yields. Thus,

$$\mathrm{RY_w} = \mathrm{P_w}/\mathrm{M_w},$$

where $\mathrm{P_w}$ is the polyculture wheat yield and $\mathrm{M_w}$ is the monoculture wheat yield.

We used mean monoculture alfalfa and wheat yields as denominators in the LER calculations[7]. To calculate LERs in the strip-crop treatment, the sum of the relative yields for alfalfa and wheat were halved, because only half of each strip-cropped plot was devoted to each species. If LER values are greater than one, intercrops are more productive per unit area than monocultures.

Nitrogen analyses

As a gauge of long-term soil fertility, total soil organic nitrogen (N) was determined for all five treatments. Soils were sampled at 6-week intervals over the growing season during both 2001 and 2002. Five cores were extracted from the top 10 cm of soil in an 'X' pattern from each plot, excluding plots in the strip-cropped treatment. In the strip-cropped treatment, four samples were collected each from wheat strips (till) and from alfalfa strips (no-till) in a grid pattern. Nitrogen concentrations were determined by the Micro-Dumas combustion method[20], using a Carlo Erba C/H/N analyzer (NA1500 C/H/N Analyzer, Carlo Erba Strumentazione, Milan, Italy). Nitrogen concentration values are presented on a nonvolumetric basis. Bulk density estimates in no-till wheat (1.15 g $\mathrm{cm^{-3}}$), no-till alfalfa (1.25 g $\mathrm{cm^{-3}}$) and tilled wheat (1.10 g $\mathrm{cm^{-3}}$) were so similar that the maximum error for not weighting nitrogen comparisons with bulk density estimates is 5% or less, and would underestimate any differences observed.

Percent N values were $\arcsin\sqrt{(x/100)}$ transformed prior to analysis. This standard transformation allows percentages to be analyzed with parametric statistics[21]. Because repeated-measures ANOVA revealed significant interactions between date and treatment, an ANOVA was performed on total N concentrations for each individual sampling date. Wheat grain from both years was also analyzed for protein concentration. To calculate crude protein concentration, we multiplied percent N values by constants, according to the methods of the Association of Organic and Analytical Chemists[20].

Abundance of selected arthropod pests and predators

Two trapping stations were situated near the center of each plot. A pan trap was located at each station (i.e., six traps per treatment). Pan traps consisted of yellow plastic bowls affixed to wooden posts that were adjusted when needed to maintain the bowl rims level with the crop canopy. A mixture of water and ethylene glycol was used to cover the bottom of each pan trap

Pan traps were emptied 5 days after the ethylene glycol–water mixture was added. Traps were collected seven times during 2001 and five times during 2002. Arthropods were also collected with a sweep net on three dates during 2002. Samples consisted of 25 sweeps along a randomly selected transect in each experimental plot. Most results are

presented for abundance at the family level because counts of individual species were low.

Differences in mean abundances of herbivorous and predatory arthropod populations among treatments for pan traps were analyzed for each season by repeated-measures ANOVA. Arthropod count data were square-root transformed prior to analysis[21]. Because the year × treatment interaction was significant for most arthropod groups, data are presented as means for each season. ANOVAs were also performed on data collected from sweep nets. Sweep sample data were analyzed for each of three sampling dates (25 May, 13 June and 18 July). These three dates represent three distinct stages of the growing season (i.e., before the first alfalfa harvest, before the wheat harvest, and after the second alfalfa harvest); population sizes of arthropods were therefore quite variable among dates.

Results and Discussion

Above-ground biomass and intercrop advantage

Because crop productivity is the main goal of production agriculture[22], one of the factors in agroecology receiving considerable attention is harvestable biomass. In 2001, total above-ground biomass for all treatments, except the no-till alfalfa–wheat intercrop, averaged approximately 7000 kg ha^{-1}, and biomass for the no-till intercrop treatment was approximately 5500 kg ha^{-1}. Biomass values were lower in 2002, ranging from about 6000 kg ha^{-1} for wheat monoculture, alfalfa monoculture, and conservation-till alfalfa–wheat intercrop treatments to 4500 kg ha^{-1} for the no-till alfalfa–wheat intercrop treatment. According to Knapp et al.[23], tallgrass prairie biomass in North America has been estimated to be about 4000 kg ha^{-1}; one estimate for the Konza Prairie in Kansas was given as 5200 kg ha^{-1} [24]. Total biomass estimates from our experimental treatments were generally higher than these grassland values; the no-till intercrop was the only system that produced lower biomass than natural grassland ecosystems.

In 2001, significant differences in wheat grain yields (Table 1) were observed among different treatments ($P < 0.001$). Wheat monoculture and alfalfa–wheat strip-crop treatments had similar grain yields (3749 and 3644 kg ha^{-1}, respectively). The no-till alfalfa–wheat intercrop yielded significantly less than all other treatments containing wheat; it was also the only treatment that did not exceed the 2001 average Kansas winter wheat yield (2757 kg ha^{-1}). In 2002, wheat monoculture again produced the highest grain yield ($P < 0.001$). Both the wheat strips in the alfalfa–wheat strip-crop and the conservation-till alfalfa–wheat intercrop produced similar yields. No-till alfalfa–wheat again had the lowest grain yield. All grain yields were lower in 2002 than in 2001, presumably due to drought conditions in 2002.

Alfalfa harvested per unit area in 2001 (Table 2) was greatest in alfalfa strips (in alfalfa–wheat strip-crop) and alfalfa monocultures ($P < 0.001$) compared to other treatments. Small amounts of alfalfa were harvested in wheat strips and wheat monocultures, presumably due to the field being in continuous alfalfa cultivation for 4 years prior to planting wheat. Alfalfa biomass harvested in 2002 was greater in alfalfa monoculture ($P < 0.001$) than conservation-till alfalfa–wheat intercrops, alfalfa strips (in alfalfa–wheat strip-crop) and no-till alfalfa–wheat intercrops.

Alfalfa was more productive in 2002, during drought conditions, when intercropped. In 2002, alfalfa yields in the conservation-till alfalfa–wheat intercrop treatment were slightly higher than alfalfa yields for this treatment in 2001; alfalfa production was reduced during the drought only in the alfalfa monoculture and alfalfa strips within the alfalfa–wheat strip-crop. Perhaps decreased competition for water in intercrops led to higher forage yields[9] because alfalfa's long taproot can compete vigorously for water during a drought.

Mean weed biomass was small in 2001 compared to 2002 (Table 3). In 2001, weed biomass was significantly greater in the alfalfa monoculture ($P < 0.01$) compared to other treatments. Mean weed biomass in 2002 was significantly greater in the alfalfa monoculture and no-till alfalfa–wheat intercrop treatments ($P < 0.001$) compared to other treatments. The wheat monoculture treatment had the lowest weed biomass, presumably due to 2 years of continuous tillage. This low competition from weeds likely contributed to the high seed yield.

Table 1. Wheat grain biomass harvested ($x \pm$ SE).

Treatment	2001 Grain (kg ha^{-1})	2002 Grain (kg ha^{-1})
Wheat monoculture	3749 ± 163 a	2107 ± 229 A
Wheat strips (in strip crop)	3644 ± 212 a	1318 ± 127 B
No-till alfalfa–wheat	1497 ± 127 c	460 ± 92 C
Conservation-till alfalfa–wheat	2948 ± 83 b	1286 ± 97 B
Alfalfa monoculture	0	0

Mean yields were analyzed by year. Different letters indicate significant differences ($P < 0.001$).

Table 2. Alfalfa hay biomass harvested ($x \pm$ SE).

Treatment	2001 Alfalfa (kg ha^{-1})	2002 Alfalfa (kg ha^{-1})
Wheat monoculture	224 ± 67 d	0
Wheat strips (in strip crop)	351 ± 65 d	0
Alfalfa strips (in strip crop)	6773 ± 264 a	2147 ± 208 B
No-till alfalfa–wheat	1847 ± 197 b	2121 ± 316 B
Conservation-till alfalfa–wheat	1261 ± 73 c	2379 ± 103 B
Alfalfa monoculture	6298 ± 383 a	4978 ± 715 A

Mean yields were analyzed by year. Different letters indicate significant differences ($P < 0.001$).

Table 3. Weed biomass ($x \pm$ SE).

Treatment	2001 Weeds (kg ha^{-1})	2002 Weeds (kg ha^{-1})
Wheat monoculture	288 ± 127 (b)	24 ± 12 (C)
Alfalfa–wheat strip crop	267 ± 61 (b)	522 ± 70 (B)
No-till alfalfa–wheat	144 ± 29 (b)	1012 ± 150 (AB)
Conservation-till alfalfa–wheat	101 ± 29 (b)	334 ± 61 (BC)
Alfalfa monoculture	747 ± 173 (a)	1154 ± 309 (A)

Mean yields were analyzed by year. Different letters indicate significant differences ($P < 0.01$).

Table 4. Average land equivalent ratio (LER) values calculated using mean wheat and alfalfa monoculture yields.

	RY_a		RY_w		LER	
Treatment	2001	2002	2001	2002	2001	2002
SC	1.08	0.44	0.97	0.62	1.03[1]	0.53
NT	0.29	0.43	0.40	0.22	0.69	0.65
CT	0.20	0.48	0.79	0.61	0.99	1.09[1]

RY_a represents the relative yield of alfalfa, and RY_w, the relative yield of wheat.
Treatment SC is strip-cropped alfalfa and wheat. Treatment NT is no-till alfalfa–wheat row intercrop. Treatment CT is conservation-till alfalfa–wheat row intercrop.
[1] LER values greater than 1 indicate overyielding.

Weeds represented a larger percentage of harvested biomass in the alfalfa monoculture, perhaps because this treatment received no tillage, compared to other treatments. Low weed mass from the conservation-till alfalfa–wheat intercrop corresponds to results reported by Carr et al.[25], who found that a wheat–lentil intercrop canopy intercepted much of the photosynthetically active radiation that would otherwise reach soil and weeds.

In 2001, the strip-cropped alfalfa–wheat intercrop had the highest land-use efficiency (Table 4) with a mean LER value of 1.03 ± 0.03, suggesting that this treatment was as productive as if the land was divided into two monocultures. Intercrop advantage was more visible in 2002, during drought conditions. The conservation-till alfalfa–wheat intercrop treatment showed a possible intercrop advantage with a mean LER of 1.09 ± 0.10. Thus, total productivity per unit area in this treatment is comparable to that of monocultures, perhaps due to complementary use of resources such as water and nitrogen. Putnam and Allan[8] suggested that border rows in a sunflower–mustard strip-crop benefitted from excess N and water; mustard (*Brassica hirta* Moench) and sunflower (*Helianthus annuus* L.) had low interspecific competition due to temporal differentiation of resource requirements.

Low yields and LER values in the no-till alfalfa–wheat intercrop contradict findings of others who have reported higher yields for no-till than for conventionally tilled systems[26,27]. However, weeds were suppressed with herbicides in those studies, and interaction effects of intercropping and tillage were not considered. Because alfalfa was never tilled in the no-till intercrop, this species was at least 0.25 m taller than wheat plants, especially in 2002. Wheat plants therefore received reduced sunlight.

Soil nitrogen

Manufacture of nitrogen fertilizer uses more energy than all other parts of production agriculture[28], and much applied N is leached out of the system[29]. To create less energy-intensive systems, nitrogen-use efficiency must be increased by management systems that improve efficient means of fertilization, such as nutrient recycling and retention. Alfalfa–wheat intercrops have the potential for not only reduced interspecific competition via complementary resource use, but also facilitation of wheat growth associated with the legume's contribution of nitrogen[9,30].

Blair et al.[31] reported that the upper 25 cm of soil at the Konza Prairie contains about 625 g N m^{-2}; assuming a bulk density of 1 g cm^{-3}, this is a concentration of about 0.25% N. Soils in our experimental treatments, although quite fertile, had much lower N concentrations than the soil at Konza Prairie.

Figure 1 depicts total soil N concentration (g kg^{-1}) over two growing seasons including six sampling dates. Because all treatments were in continuous alfalfa for 4 years prior to this experiment, concentrations of soil N were fairly high compared to non-nitrogen-fixing systems. Thus, fewer significant trends emerged during the first season than in the second season.

In contrast, significant differences were observed among treatments during 2002. Soil nitrogen concentration tended to increase from the previous year in those treatments containing high percentages of alfalfa. In April and June, wheat monoculture and wheat strips in the alfalfa–wheat strip-crop had significantly lower concentrations of mean soil N compared to other treatments (April, $P < 0.001$; June, $P < 0.001$). In July 2002, wheat monoculture and both wheat and alfalfa strips in the alfalfa–wheat strip crop had lower mean soil N concentrations than the alfalfa monoculture and two row-intercrop treatments ($P < 0.001$). The low soil N in wheat strips within the alfalfa–wheat strip-crop indicates that alfalfa strips do not contribute significant N to wheat strips. Brophy et al.[32] determined that the maximum distance of N transfer from legumes to grasses was only 20 cm. Strips in the alfalfa–wheat strip-crop were over 3.6 m wide, so that beneficial edge effects were probably not realized for soil in wheat strips.

Soil N concentrations in the wheat monoculture were maintained between years. Soil in the wheat monoculture contained approximately 1890 kg N ha^{-1} to a 10 cm depth. Assuming that only 1–2% of the total soil N is in readily available forms of nitrate and ammonium[33], and much of the N is removed when wheat is harvested, this system likely will not be able to support current levels of production for more than one or two additional growing

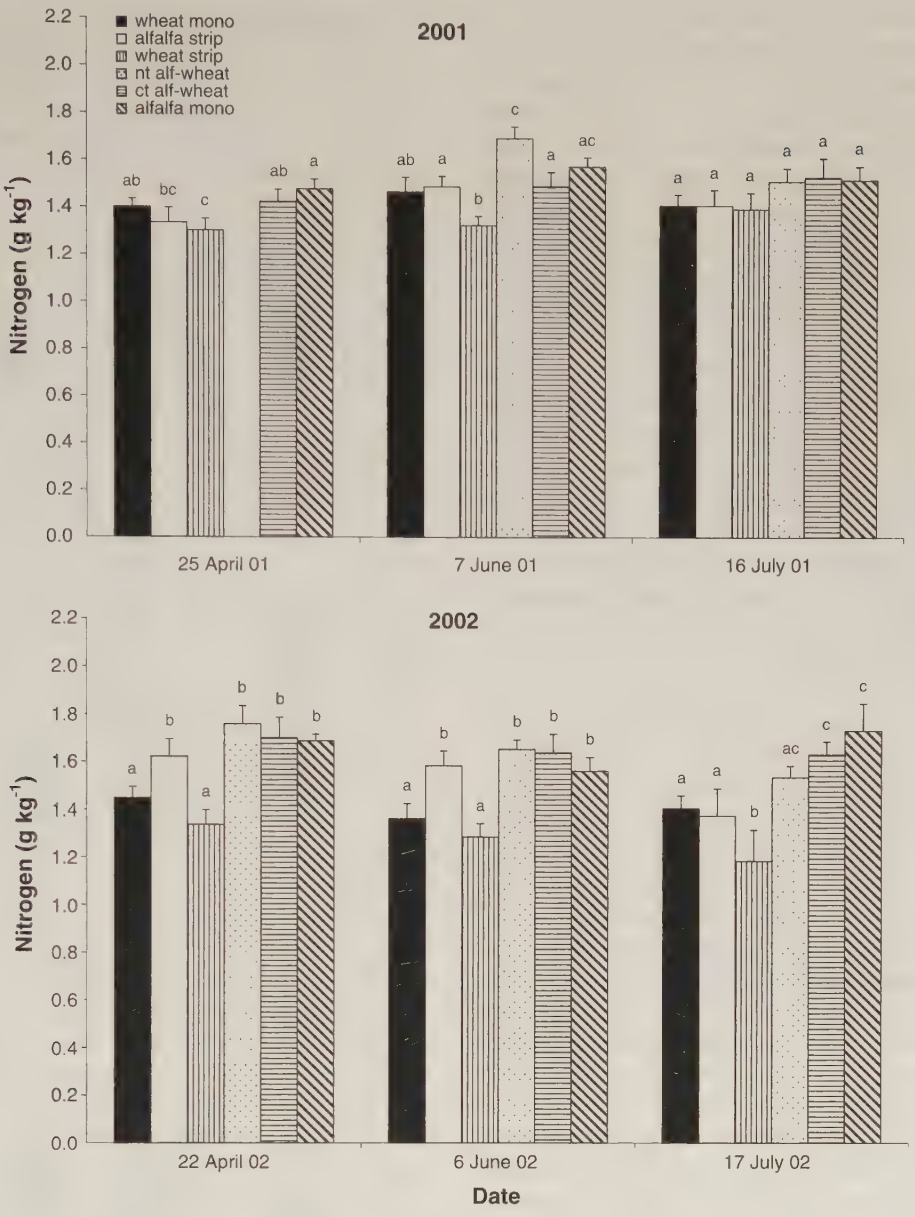

Figure 1. Mean soil nitrogen concentration ($x \pm$ SE) presented as ($g\,N \cdot kg\,soil^{-1}$). Different letters above treatment means indicate significant differences ($P \leq 0.05$) on a particular sampling date. Wheat monoculture is represented by black bars; alfalfa strip in alfalfa–wheat strip-crop, by white bars; wheat strip in alfalfa–wheat strip-crop, by vertically striped bars; no-till alfalfa–wheat intercrop, by dotted bars; conservation-till alfalfa–wheat intercrop, by horizontally striped bars; and alfalfa monoculture is represented by diagonally striped bars.

seasons, including mineralization of soil organic matter. In contrast, the alfalfa monoculture, no-till intercrop, and conservation-till intercrop treatments should be able to supplement their own fertility indefinitely without external N inputs, assuming that alfalfa fixes 150–250 $kg\,N\,ha^{-1}$ year[33]. However, alfalfa monoculture is certainly not a sustainable system; increased temporal and spatial diversity should be incorporated to increase resilience against pest build-ups and autotoxicity.

The no-till intercrop treatment exhibited high soil N concentrations and low primary productivity, whereas the wheat monoculture and wheat strips (in the alfalfa–wheat strip-crop) were characterized by high grain production and lower soil N. Our results support conclusions drawn by other researchers who found that soil N and crop productivity may be unrelated[31,34]. We found, however, that total N appeared to be inversely related to net primary productivity.

Grain nitrogen

Percent crude protein values averaged 12.4% in 2001 and 15.8% in 2002. These protein values are well within the range of acceptable grain protein values. The average

wheat protein concentration for the past 10 years in Kansas is about 12%[35].

No effect of treatment on grain protein concentration was observed. Soil N appeared to have little influence on wheat grain quality. Soil N concentrations throughout the field seemed to be sufficient for high wheat grain nitrogen concentrations without the use of fertilizers during the experiment. However, it should be noted that we measured total N and not plant-available nitrogen.

Arthropods

Insect pests collected in pan traps and sweep nets included leafhoppers (Hemiptera: Cicadellidae), aphids (Hemiptera: Cicadellidae), grasshoppers (Orthoptera: Acrididae) and alfalfa weevils (*Hypera postica* Gyllenhal). We expected that wheat and alfalfa monocultures would experience greater pest pressure than would intercrops, based on the strong support for Root's resource concentration hypothesis[12,14,36]. Because our field site was in continuous alfalfa for 4 years preceding the study, alfalfa-feeding insects were already present in the field. However, wheat-feeding insects were much less abundant. In this study, alfalfa may be considered the host plant and wheat the nonhost plant, or interference crop.

Leafhoppers *Ceratagallia agricola* Hamilton, *C. uhleri* Van Duzee and *Paraphlepsius irroratus* (Say), all of which feed on alfalfa and other legumes, were common in both years. Leafhoppers in pan traps were significantly more abundant in the alfalfa monoculture and no-till alfalfa–wheat intercrop treatments in 2001 ($P < 0.05$) and in the alfalfa monoculture in 2002 ($P < 0.001$) than in other treatments (Fig. 2a). No strong trends in leafhopper numbers were observed from samples collected by sweep net.

Aphid trends were not significant in 2001, but in 2002 they were similar to those for leafhoppers (Fig. 2b). The most common aphid species during 2001 was the spotted alfalfa aphid, *Therioaphis trifolii* forma *maculata* (Buckton). This species recurred in 2002, but pea aphids, *Acyrthosiphon pisum* (Harris), were also in fairly large numbers. Differences among treatments were not significant for pan traps in 2001; in 2002 aphid abundances were greater for no-till alfalfa–wheat intercrop, conservation-till alfalfa–wheat intercrop, and alfalfa monoculture treatments than for wheat monoculture and alfalfa–wheat strip-crop treatments ($P < 0.05$). In general, the treatments with the largest concentrations of alfalfa also had the highest numbers of aphids. Few strong trends were exhibited by sweep net samples. However, aphid numbers from sweep samples were significantly lower in wheat strips than in alfalfa strips over all three sampling dates in 2002. If the 3.6 m-wide strips are analogous to wheat monocultures, these results are not surprising, based on wheat monoculture findings.

Grasshoppers were only examined during the second growing season, when large numbers indicated that they were a potential pest problem. Grasshoppers occur in great numbers when climatic conditions are hot and dry, as they were in 2002[37]. The most common grasshopper species found was *Melanoplus sanguinipes* (Fabricius). No significant differences in grasshopper abundance were observed among treatments for any of the three sampling regimes.

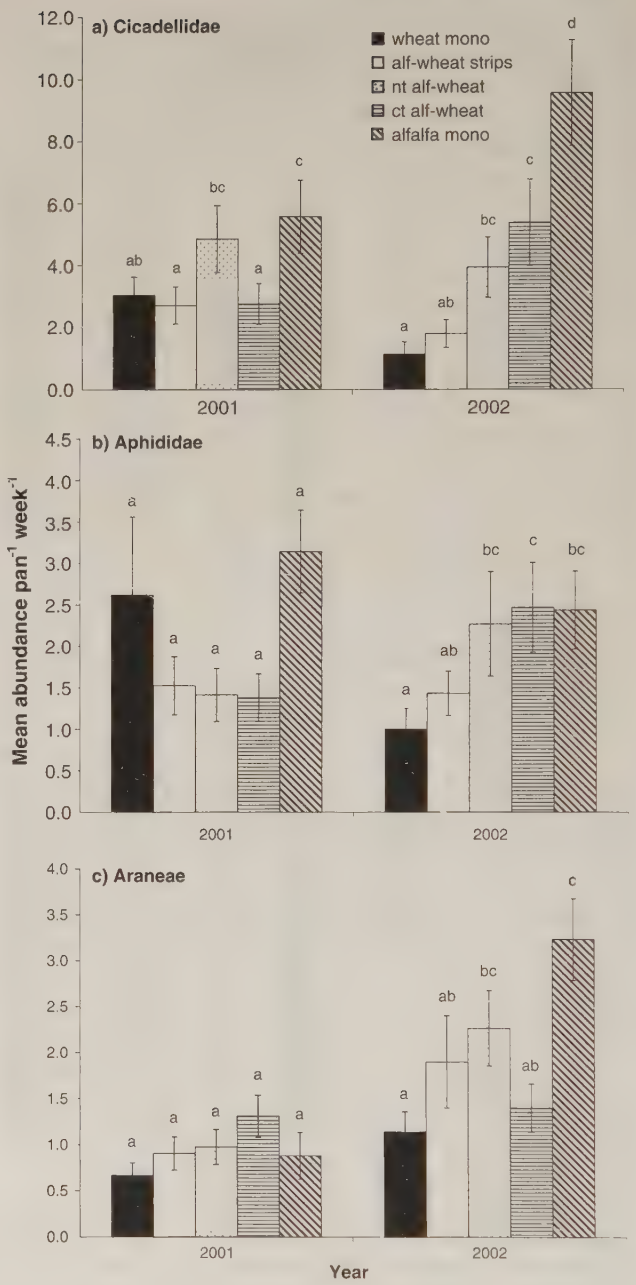

Figure 2. Mean abundances ($x \pm$ SE) for herbivorous arthropod groups: (a) leafhoppers; (b) aphids; and (c) spiders, collected in pan traps. Unless otherwise noted, different letters above treatment means indicate significant differences ($P \leq 0.05$). Note that the scales of the *y*-axes differ. Wheat monoculture is represented by black bars; alfalfa–wheat strip-crop, white bars; no-till alfalfa–wheat intercrop, by dotted bars; conservation-till alfalfa–wheat intercrop, by horizontally striped bars; and alfalfa monoculture is represented by diagonally striped bars.

Thus, this herbivorous species appeared to function as a generalist within this diverse research design.

The final herbivorous species included in this study was the alfalfa weevil (*Hypera postica* Gyllenhal), analyzed solely from the 25 May 2002 sweep samples. Alfalfa weevil numbers are typically greatly reduced by the first cutting; thus they are only injurious early in the growing season. Weevils were rare in 2001, but were numerous in 2002. Alfalfa strips in the alfalfa–wheat strip-crop had higher densities (36 weevils per 25 sweeps) than other treatments ($P < 0.001$) with the exception of alfalfa monoculture, which also had a mean abundance (18 weevils per 25 sweeps) similar to the no-till alfalfa–wheat intercrop (7 weevils per 25 sweeps). Because alfalfa weevils prefer to feed on, and will reproduce only on, alfalfa[38], incorporation of nonhost plants, such as other forage species that could be harvested with alfalfa for hay, into alfalfa strips should decrease weevil population densities.

Ladybird beetles are a common aphid predator and are, therefore, of interest as a biological control mechanism. The most common species found was *Coccinella septempunctata* L. Differences on any sampling date were not significant because numbers caught were very low. However, repeated measures analysis for pan traps indicated that alfalfa–wheat strip-crop and conservation-till alfalfa–wheat intercrop treatments tended to have greater abundances of ladybird beetles ($P < 0.05$), than monocultures.

Total spider abundance (Fig. 2c) was calculated for all sampling regimes. Pan catches were significantly different among treatments in 2002 only; total spider numbers were highest in alfalfa monoculture ($3.2\,\text{pan}^{-1}\,\text{week}^{-1}$) and no-till alfalfa–wheat intercrop ($2.3\,\text{pan}^{-1}\,\text{week}^{-1}$) treatments ($P < 0.05$). Differences were also significant for the June 2002 sweep samples, when no-till (16.0 per 25 sweeps) and conservation-till (10.7 per 25 sweeps) intercrop treatments had higher spider densities than all other treatments ($P < 0.05$). Spiders are one of the main predaceous (i.e., tertiary consumers) taxa, important as a regulatory species in numerous agroecosystems[39].

Two possible reasons for high spider numbers in the no-till alfalfa–wheat intercrop are high prey densities[13] and low soil disturbance[40]. Stinner et al.[40] also suggested that predatory arthropods may inhabit no-till systems due to microhabitat conditions created by the surface litter. While no-till fields may encourage invertebrate pests, high faunal diversity in no-till systems may also foster biological control[41].

In general, arthropod population trends in no-till alfalfa–wheat intercrops were similar to those in alfalfa monocultures. The high numbers of leafhoppers in 2001 and aphids in 2002 in pan traps are attributed to the high amount of alfalfa present[42]. Due to the close alfalfa–wheat association in the no-till intercrop treatment, wheat plants were unlikely to deter alfalfa specialists from finding nearby alfalfa plants.

Our results support Root's resource concentration hypothesis. When pest numbers were significantly different among treatments, those treatments with the highest proportions of alfalfa had the highest numbers of herbivorous arthropods. However, these trends were not significant across all dates and sampling methods. Results do not support the enemies hypothesis. Natural enemy population trends were rarely significant; therefore no general statements can be made.

While no single intercropped treatment exhibited consistent advantages over monoculture treatments, significant differences among the various parameters measured were observed. Throughout both years, the no-till intercropped system produced the least above-ground biomass. Alfalfa performed much better than wheat during the drought; therefore treatments containing alfalfa yielded higher biomass during the second year of study. Higher soil N concentrations were observed in those treatments containing the greatest proportions of alfalfa. However, those treatments containing high proportions of alfalfa also attracted higher numbers of herbivorous keystone species.

Conclusions

The alternative agroecosystems discussed here add to the growing body of research focusing on intermediate steps between conventional agriculture and alternative systems of production, such as the perennial polyculture systems being developed at the Land Institute[43,44]. In general, the no-till intercrop system was not advantageous when compared to the other treatments, mostly due to low yields and relatively large populations of leafhoppers and aphids. The alfalfa–wheat strip-crop treatment demonstrated yields similar to alfalfa and wheat monoculture yields. However, benefits to soil N concentrations from strip-cropping alfalfa and wheat were not apparent. The conservation-till intercrop treatment was an intermediate intercrop design between the alfalfa–wheat strip-crop and no-till alfalfa–wheat intercrop treatments. Benefits of the conservation-till intercrop include overyielding in 2002 and high soil N. It appears that moderate tillage combined with a close association of dissimilar crop species can be quite productive, despite low subsidy inputs of fertilizers and fossil fuels.

Results may have differed if pesticides and fertilizers were applied. Fertilizer additions would likely have increased soil N concentrations in wheat monocultures and wheat strips in the alfalfa–wheat strip-crop, which may have resulted in increased grain nitrogen concentrations. Use of pesticides would have also altered our results. Applying a selective herbicide to the no-till intercrop treatment would have stunted alfalfa growth and therefore would probably have benefitted wheat growth and production. Also, lower alfalfa concentrations in the no-till intercrop, due to herbicide use, may have discouraged arthropod pests.

We expect that over time these agroecosystems would remain with less biotic diversity (genetic, species and patch) than natural grassland ecosystems. Although primary

production was higher in experimental treatments than in neighboring prairie, our treatments may become less productive than natural prairie systems due to lower soil N values and higher pest pressures. Perhaps incorporating several crop species into alternative agroecosystems would encourage more complete use of resources and increase resistance to pests. This design was intended to be a step between conventional agriculture and natural systems agriculture[43]. We feel that benefits accrued merit further research regarding how to solve *problems in agriculture* (e.g., high use of subsidies, pest outbreaks in monoculture systems and soil erosion), in order to solve the *problem of agriculture* by using native perennial species, encompassing natural ecosystem processes into agroecosystem management.

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Breeding for organic and low-input farming systems: An evolutionary–participatory breeding method for inbred cereal grains

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Abstract

Organic and low-input farmers often plant seed varieties that have been selected under conventional practices, traditionally including high inputs of artificial fertilizers, crop protection chemicals and/or water. In addition, these crops are often selected in environments that may or may not represent the local environment of the farmer. An evolutionary participatory breeding (EPB) method emphasizes the utilization of natural selection in combination with site-specific farmer selection in early segregating generations of a heterogeneous crop population. EPB is a combination of two specific breeding methods, evolutionary breeding and participatory plant breeding. Evolutionary breeding has been shown to increase yield, disease resistance, genetic diversity and adaptability of a crop population over time. It is based on a mass selection technique used by farmers for over 10,000 years of crop improvement. Participatory plant breeding programs originated in developing countries to meet the needs of low-input, small-scale farmers in marginal environments who were often overlooked by conventional crop breeders. The EPB method is an efficient breeding system uniquely suited to improving crop varieties for the low-input and organic farmer. The EPB method utilizes the skills and knowledge of both breeders and farmers to develop heterogeneous landrace populations, and is an effective breeding method for both traditional and modern farmers throughout the world.

Key words: plant breeding, bulk breeding, sustainable agriculture, landrace, yield, disease, quality, ecological agriculture

Introduction

Genetically uniform varieties developed by standard pedigree breeding methods dominate commercial production in many self-pollinated crops due, in large part, to their high yields and wide geographic adaptability[1,2]. These varieties perform optimally when they are grown in favorable environments and under high-input agronomic systems. However, they typically do not perform well in marginal environments or without the external inputs with which they were selected[2,3]. Serving the needs of producers in these marginal environments, whose farm conditions and practices minimize chemical inputs, has become a critical challenge to public plant breeders.

The global growth in the sales of certified organic products has increased by an average of 20–25% per year since 1990[4]. Organic farmers rely on varieties bred and selected under conventional methods that often include the use of synthetic pesticides and fertilizers, options not available under organic certification standards. Worldwide, an estimated 1.4 billion people are dependent on traditional agricultural systems characterized by marginal agricultural environments and limited use of external inputs[5]. These two groups represent a diverse array of farming systems in both developed and developing countries throughout the world. Future increases in agricultural stability and productivity may depend on increasing yields in these low-input and organic farming systems.

In organic and low-input agriculture, where synthetic pesticides and fertilizers are not applied due to regulatory or socio-economic reasons, genetic variation is the primary mechanism for buffering environmental fluctuations and maintaining important traits such as yield stability, resistance to pathogens and adaptation to low soil fertility. For this reason, many small-scale, low-input farmers have not wholly embraced homogeneous modern cultivars, choosing instead to rely on a diverse collection of local varieties and landraces[6]. Landraces are heterogeneous crop populations developed over time through both farmer selection and evolutionary processes. Additionally, a farmer's particular

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cultivar preference may vary according to characteristics such as farm size, family structure, gender, wealth and market opportunities[7].

This paper will demonstrate the practicality and unique suitability of evolutionary–participatory breeding (EPB) for low-input and organic farming systems. Yield, disease resistance and quality are important factors in developing bulk populations and these will be discussed along with an appropriate breeding scheme designed to utilize genetic diversity and farmer-assisted natural selection in small grain cereals.

An Evolutionary–Participatory Breeding Method

Evolutionary breeding (EB) is based on a mass selection technique used by farmers for over 10,000 years of crop improvement. Results of EB studies in composite cross populations of barley have shown that traits relating to reproductive capacity, such as higher seed yields, larger numbers of seeds/plant and greater spike weight, increase in populations due to natural selection over time[8,9]. These barley composite cross populations were grown annually at the University of California at Davis under standard agricultural conditions and harvested in bulk at maturity without conscious selection. The environments in which these populations were grown fluctuated from year to year in terms of temperature, rainfall and irrigation, and reflected standard regional barley-growing conditions. In barley composite cross II (CC II), reproductive capacity kept performance within 95% of the highest yielding varieties for over 50 generations[8]. Natural selection in these populations strongly favored the higher-yielding genotypes due to a positive correlation between the yielding ability of an individual and its fitness components. Jain[10] noted three components of fitness in plants: ability to germinate, survival to reproductive age and the number of seeds produced[10]. Each one of these characteristics most likely is determined by a large number of genetic and environmental factors. Natural selection acting upon segregating genotypes leads to higher fitness by identifying individuals that possess the ideal combinations of these three components of fitness.

The diversity of cultural practices among low-input and organic growers represents a considerable challenge for breeders interested in serving these farmers, since within a given agro-climactic zone, different farmers may employ very different approaches to fertility and pest management. It becomes economically impractical to subject test plots within a breeding station to the many different pressures that these diverse cultural practices present to the crop.

The EB method allows for a cost-effective procedure for selecting specific traits in a large number of plants within multiple populations grown on different farms. Genetic diversity is inherent in bulk populations that have been produced from multiple crosses of genetically variable parental germplasm. This can ensure that the population contains genotypes appropriate for each cultural practice employed within an agro-climatic zone.

Participatory plant breeding (PPB) was developed over the past 20 years to meet the needs of low-input, small-scale farmers in marginal environments often overlooked by conventional crop breeders. PPB emphasizes collaboration between breeders and farmers to share knowledge and skills to identify and improve suitable cultivars previously unavailable to low-input farmers. Until recently, PPB programs focused on cultivar trials on individual farms to identify which cultivars performed best in each locality. As PPB programs progressed, traditional low-input barley farmers in Syria were shown to be uniquely capable of identifying and selecting the highest yielding varieties on their own farms[11]. Ceccarelli et al.[11] concluded that formal plant breeding has nothing to lose and much to gain by including farmers in the selection process, and participatory plant breeding recognizes that it is farmers who ultimately decide whether or not to adopt a new variety. These programs were limited by the large number of farms in a wide range of dissimilar target environments. Both the diversity of bulk populations and the economy of the breeding procedure make evolutionary breeding methods uniquely suited for farmer participation to develop varieties for low-input and organic farming systems.

The EPB method utilizes the evolutionary force of natural selection on genetically diverse populations with active site-specific farmer selection. It combines the beneficial attributes of EB and PPB to expose maximum genetic variation to a target environment to develop agronomically and culturally adapted crop populations. Constant fluctuations in stressful environmental conditions favor a genetically flexible population capable of evolving multiallelic associations with multiple adaptive peaks[12].

Yield, Disease Resistance and Quality

Can an EPB method reliably produce high-yielding, disease-resistant cultivars of desired quality while maintaining a high degree of adaptability to fluctuating environmental conditions? Numerous studies have focused on three important crop components—yield, disease resistance and quality—in ways that allow for maximization of these components within an effective EPB process.

Yield

Yield is a quantitative trait influenced by numerous genetic and environmental factors. Parental selection and progeny yield prediction are important tools for the breeder to utilize when developing an initial EPB population. Early generation population means of unselected inbred lines may occasionally deviate from their mid-parent values, but typically the differences are small[13–16]. Busch et al.[14] evaluated the performance of crosses between high-yielding parents (high × high), high- and low-yielding parents (high × low), and low-yielding parents (low × low). In 21

randomly selected F_2-derived F_5 and F_6 lines over 2 years, the progeny of the high × high, high × low, and low × low crosses produced an average of 343, 321 and 293 g/plot respectively. Utz et al.[16] concluded that parental means can be applied successfully for predicting the usefulness of their crosses. If no information about the parents exists, Schnell[17] points out that it should be more economical to test n parents instead of progenies of the $n(n-1)/2$ possible crosses.

Yield during periods of drought tends to favor bulk populations over commercial cultivars selected under high-input systems, though these yield advantages do not hold when conditions are agronomically favorable[1]. Soliman and Allard[2] reported that the majority of modern barley cultivars responded more positively in terms of yield to favorable environments, whereas the barley composite crosses were significantly more stable than the commercial cultivars across a range of environments. This reflects both the favorable environments where these modern barley cultivars were selected and the value of the genetic diversity in the composite cross populations in maintaining yield stability in the physical and cultural environments not represented through the centralized breeding process. To maintain yield stability, the bulk population must remain genetically diverse[2]. In the case of increased homozygosity leading to lower yield stability over varying environments, breeders could upgrade existing populations by continually incorporating modern elite material[1].

Degago and Caviness[18] found that the bulk breeding method is more effective in increasing yield when there is a constant year-to-year selection pressure from a disease or other stress factors. What then is the influence of natural selection on yield in inbred bulk populations when selection pressure is not constant during each reproductive cycle? Corte et al.[19] evaluated yield in dry bean harvests for up to 17 successive generations under conditions that differed significantly in temperature, rainfall and day length. The segregating bulk populations had large variation for traits related to competition, such as growth habit, maturity and seed size. They found a mean yield gain of 2.5% per generation over the mean of the parents. This indicates that natural selection will favor high-yielding genotypes in environments with fluctuating biotic and abiotic selection pressures, a condition typical of most agroecosystems. This flexibility is especially useful in farming systems that do not rely on crop protection chemicals and high fertilizer inputs.

Disease resistance

A major problem with monocultures of varieties grown over a geographically large area is the difficulty in the control of persistent and flexible plant diseases[20]. Simply increasing the genetic diversity within a monoculture through the use of multilines has been shown to be an effective strategy for limiting the severity of yield reductions due to disease[21–23]. Aside from affording this level of crop protection, a genetically diverse bulk population allows for adaptation to disease through the establishment of a self-regulating plant–pathogen evolutionary system[24]. The self-regulating population functions in the following way: pressure from the pathogen requires a genetic shift in the host population to minimize losses in reproductive capacity and yield. In turn, the pathogen population must evolve new genetic strategies that allow it to survive each year[24]. This type of plant–pathogen self-regulation is a characteristic of genetically diverse populations and is generally not found in homogeneous, homozygous monocultures.

Examples from evolutionary breeding in barley demonstrate the self-regulating capacity of a diverse bulk population. Two studies looking at frequencies of resistance to scald, *Rhynchosporium secalis*, in barley composite cross populations II and V, found that the appearance, disappearance and reappearance of different family types over successive generations represented responses to biological stress caused by the variable and shifting pathogen population[25–27]. The main feature of the changes was a reversal of an excess of susceptible families in the earlier generations to a greater percentage of resistant families in F_{45}[27]. Disease levels for scald in the barley composite populations II and V varied with environmental conditions year to year; however, damage caused by scald was small in each of the approximate 50 years during which these populations were grown, and showed a general trend of steadily decreasing pathogenicity[24]. Another interesting note is that, regardless of the genetic basis of resistance in the parents, the segregation and recombination that occurred in composite cross V (CC V) has given rise to numerous novel multiple-resistant genotypes[25]. This self-adjusting coevolutionary process contrasts with many commercial cultivars that incorporate single gene resistances to bring the pathogen under control, often for a short time until genetic shifts in the pathogen population overcome the resistance of the plant.

Buzzell and Haas[28], in determining the relative performance of near isogenic soybean lines as they reacted to *Phytophthora* rot, concluded that natural selection is effective when segregating populations are grown in soil where *Phytophthora* rot causes yield reductions of susceptible cultivars. For example, if resistant plants produce more seeds than susceptible plants, a bulk breeding method dependent, in part, on natural selection or farmer-assisted selection against disease is effective. Hartwig et al.[29] focused on soybean cyst nematode (SCN) infestations in bulk populations, and found that when F_5 soybean bulk populations were grown on cyst-infested soil, resistant plants increased from 5% to 40%. When the F_5 from bulk populations of soybeans were grown on uninfected soil, resistant plants remained at 5%. Similarly, results from the study by Degago and Caviness[18] indicate that the bulk breeding method for disease resistance in soybean is more effective when there is constant year-to-year selection pressure.

Two types of resistance are important to distinguish when developing a crop population: vertical, or single-gene resistance, and horizontal, or multi-gene resistance[30,31]. Single-gene or vertical resistance generally confers complete

resistance to a variety from a specific pathogen; however an evolving pathogen population more easily overcomes this type of resistance. Durable or horizontal resistance does not confer absolute resistance to a variety (there may be evidence of the pathogen on the plant); however, many genes utilizing many different resistance mechanisms are involved in control of the pathogen and therefore the variety is not easily overcome by an evolving pathogen population. In general, disease-causing pathogens are more capable of overcoming single, major gene resistances than multi-gene, durable resistances[32]. Durable resistance is therefore generally much longer lasting than single-gene resistance. The self-adjusting coevolutionary processes between plant and pathogen populations found in genetically variable crop populations provide the farmer with more stable genetic disease control and long-lasting durable resistance.

Quality

Quality is a characteristic, which, unlike yield and disease resistance, is not directly influenced by natural selection. Therefore, inclusion of high-quality parents is of particular importance when considering the quality objectives of the population. Breeding objectives for quality are shaped by the prevailing market conditions, whether local, national or international. If the crop is feed barley, for example, quality considerations will be minimal in comparison to the requirements of bread wheat destined for export.

Unless specific breeding objectives (e.g., disease resistance) justify the use of a low-quality parent, they should be avoided if a high-quality bulk population is a priority. A breeding objective for high end-use quality requires a selective genetic base of adequate- to high-quality parents[33]. In soft red wheat (SRW) bulk populations, Bruckner and Finney[33] found that the milling and baking quality of F_4 populations can effectively predict the quality of F_5 lines. This was effective if 100% of the parents were in the SRW market class. For those populations with only 50% SRW parentage, the proportions of acceptable-quality lines were much more variable and much less predictable based on F_4 bulk quality evaluation. Therefore, using appropriate parents can significantly reduce the amount of testing required in derived lines if prediction equations can be applied. An exception to this strategy would be for quality traits with known low heritability, such as flour protein concentration, which is largely affected by environmental influences[34].

Maintaining quality characteristics in a bulk population is of primary concern to growers for whom a high quality threshold is necessary to successfully market their crop and where quality testing is prohibitively expensive or timely. In the case of milling and baking quality in wheat, Kratochvil and Sammons[35] demonstrated that parental lines with unacceptable milling and baking scores should be avoided if the crossing scheme consists of only two parents. They showed that the inclusion of a parent with unacceptable quality could be sufficient to counteract the parent with high quality, resulting in unacceptable baking quality for the F_1 hybrid and subsequently for the F_2 population. In this case, the F_2 population (and subsequent generations) will include some individuals with high quality, but the population as a whole will not be of high quality.

An unselected bulk population will generally maintain a quality score approximating the mid-parent value. In evaluating sodium dodecyl sulfate (SDS)-sedimentation, a measure of gluten strength in wheat, in unselected F_4 progeny derived from crosses between wheat cultivars significantly different in sedimentation values, Utz et al.[16] showed that the mean of the progeny was not significantly different from the mid-parent values. Likewise, in an analysis of six quality traits in the unselected single-seed descent F_6 progeny of a high-quality parent (Finley) and a low-quality parent (Estica), we found the progeny mean to equal the mid-parent value for five of the six traits measured across three site years (Table 1). Only loaf volume from one site year showed a significant difference between the progeny mean and the mid-parent value.

Quality components are similar to yield components in that for both traits the mean of the progeny does not deviate significantly from the mid-parent values. The distinction between these two traits is seen in the effects of natural selection. Natural selection will improve the yield of a population, often through improved resistance to disease-causing pathogens. Natural selection will not improve the quality of a population unless the trait is genetically linked to a gene that is positively influenced by natural selection. In addition to the influence of natural selection on the population, quality traits may be inconsistent from year to year, depending on the predominant genotypes and multilocus associations. The variability within a population for certain baking and milling characteristics will have to fit within specified parameters defined by the end-use of the product. The best way to insure a high-quality population is to use high-quality parents in the crossing design. Desired quality characteristics must therefore be considered carefully before initiation of the EPB method.

Methods of an EPB Scheme

Parental selection is the single most important step in the EPB process. The most useful parental germplasms are modern cultivars and breeding lines, especially materials that are adapted to the local environment or closely similar environments[36]. Other valuable sources of parental germplasm include locally adapted cultivars and landraces produced before the modern era of high chemical inputs, and unadapted exotic germplasm containing traits or genes of interest.

For inbred grain crops, several types of crosses may be used to initiate the EPB method. Examples include: (1) a simple cross consisting of two carefully selected parents; (2) a top-cross consisting of three parents; (3) crosses of 4–10 parents that are subsequently bulked; and (4) a composite cross consisting of 11 or more parents crossed in any

Table 1. Six quality traits evaluated for progeny mean and mid-parent value in unselected single-seed-descent lines derived from a high-quality parent (Parent 1: Finley) crossed with a low-quality parent (Parent 2: Estica) in three site-locations.

	Parent 1	Parent 2	Mid-parent	Progeny mean	Progeny minimum	Progeny maximum
Site Year 1: Finley × Estica, Pullman, Washington 2003						
Wheat protein	11.1	10.2	10.65	11.13	9.30	14.40
Flour yield	66.8	65	65.90	65.04	60.50	68.70
Flour ash	0.3	0.37	0.34	0.36	0.32	0.43
Mill score	86.5	80.9	83.70	81.40	77.30	84.70
Loaf volume	815	525	670.00	635.43	470.00	845.00
Mix time	3.4	3.1	3.25	3.07	1.80	5.40
Site Year 2: Finley × Estica, Lind, Washington 2003						
Wheat protein	14.4	13.4	13.90	13.39	12.20	14.90
Flour yield	69.7	64.1	66.90	66.91	56.20	70.60
Flour ash	0.35	0.47	0.41	0.38	0.35	0.50
Mill score	86.9	74.8	80.85	82.31	72.80	85.90
Loaf volume	1035	800	917.50*	798.70*	650.00	905.00
Mix time	2.6	1.9	2.25	2.34	1.40	3.90
Site Year 3: Finley × Estica, Pullman, Washington 2002						
Wheat protein	15.4	10.1	11.97	12.09	11.30	13.50
Flour yield	63.1	66.6	65.27	64.67	61.90	69.00
Flour ash	0.44	0.36	0.39	0.38	0.34	0.42
Mill score	75.3	83.1	79.83	79.91	75.60	85.40
Loaf volume	785	680	765.00	649.38	445.00	805.00
Mix time	1.5	4.5	3.40	3.15	1.80	4.40

* Mid parent values and progeny means significant at $P < 0.05$, other values not compared; all other traits not significantly different.

number of patterns. Each crossing scheme has merits and drawbacks. In general, the more parents and greater diversity among the parents, the greater and longer lasting the genetic diversity of the population. Initial genetic diversity slows the population's tendency to achieve homogeneity, thereby delaying the eventual genetic reinvigoration of the population. Disadvantages of using a large number of parents include a potential dilution of the genetics of particularly good parents and a lengthier, more complex crossing scheme.

Regardless of the crossing scheme chosen, the basic methods involved in the establishment of bulk populations will be similar. Figure 1 shows a suggested EPB scheme. After the initial cross is made, the breeder grows out the F_1 seed in a greenhouse. F_2 seed is planted in a bulk plot in the breeder's field for seed increase, and is harvested with no conscious selection. This could proceed from F_1 plants to enough F_2 plots to yield 8–24 kg of F_3 seed. This seed is then given to the farmer to plant approximately 0.5 ha of land. The population size must be large enough to prevent a bottlenecking event from occurring. A bottleneck event can result in a severe loss of heterozygosity and many important traits may disappear from the population. For evolutionary studies of bulk populations of inbred cereal grains, a population consisting of a minimum of 10,000–20,000 individual plants is often considered sufficient[37,38]. It will be important to discuss field and time constraints with the farmer beforehand and agree to a population size that will be large enough to allow for natural selection to act as the dominant evolutionary force, but not too large for the farmer to effectively maintain within the current farming system.

Once the F_3 seed is planted, the farmer teams with natural selection to direct the course of the population. Fisher[39] showed that natural selection will increase population mean fitness over time. The farmer will aid natural selection through varying degrees of farmer-assisted selection. Examples of farmer-assisted selection include hand roguing to remove diseased or morphologically unacceptable variants and blowing or screening smaller seed away during harvest or cleaning. In this process, the farmer can spend as much or as little time as he/she finds suitable. Option A in Figure 1 depicts the EPB method in its simplest and most economical form. Each generation, the farmer will plant, select and harvest the population, bulk and mix the seed and draw a random sample from the bulk bin to plant the following season.

After three generations of natural and farmer-assisted selection (F_3–F_5) in the target environment, the individual plants in a self-pollinating species will approach 94% homozygosity. At this point, the farmer can choose to expand the breeding process beyond the bulk population by selecting plants that are better adapted to meet market demands and performing small-scale varietal trials with these pure lines. This decision should be based on both the time and effort the farmer and breeder are able to commit, and on the market's demand for specific quality characteristics. For example, in the Pacific Northwest region of the US, an organic farmer growing soft white wheat for the organic cereal

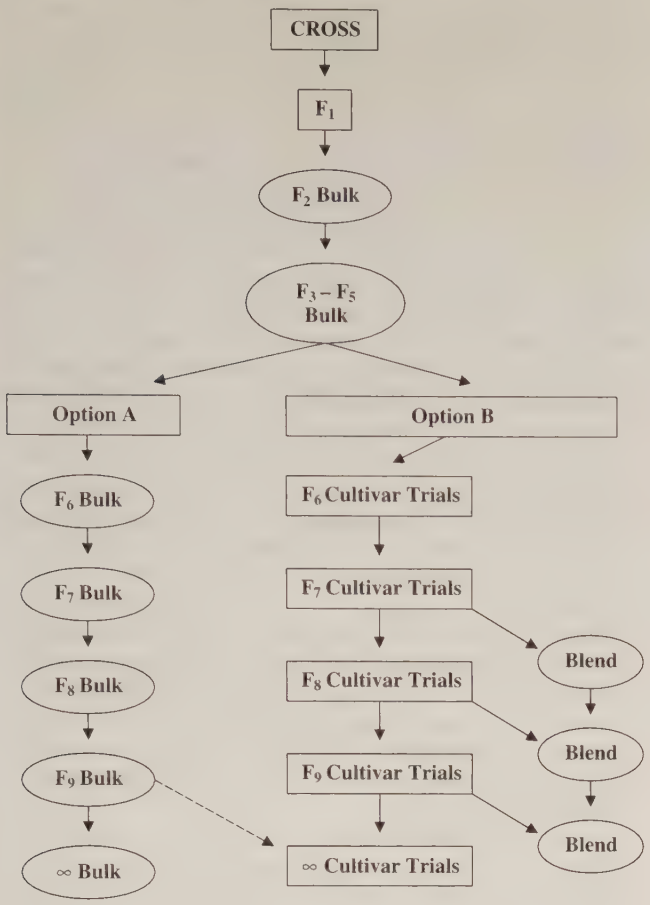

Figure 1. An evolutionary participatory breeding method.

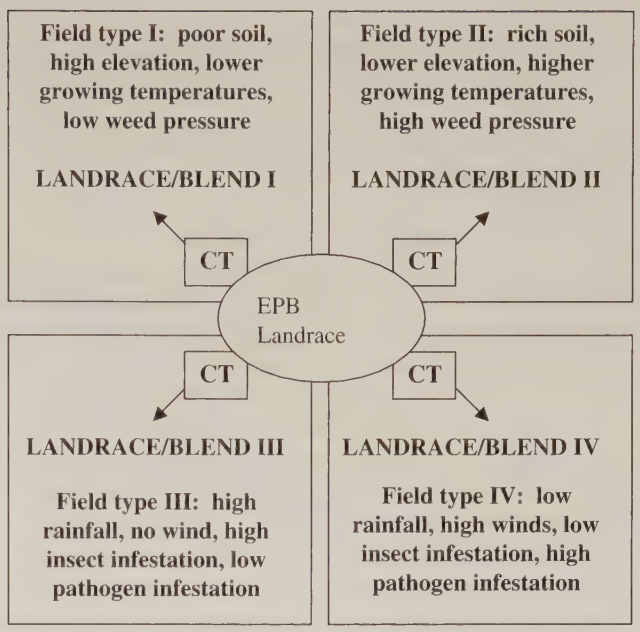
Field type I: poor soil, high elevation, lower growing temperatures, low weed pressure
LANDRACE/BLEND I
Field type II: rich soil, lower elevation, higher growing temperatures, high weed pressure
LANDRACE/BLEND II
CT
CT
EPB Landrace
CT
CT
LANDRACE/BLEND III
Field type III: high rainfall, no wind, high insect infestation, low pathogen infestation
LANDRACE/BLEND IV
Field type IV: low rainfall, high winds, low insect infestation, high pathogen infestation

Figure 2. Farmer field overview. Stratified bulk selection. EPB landrace and cultivar trials (CT) are a part of the farming system, receiving the same agricultural and environmental selection pressures as the cultivated crop.

flake market may be apathetic toward traditional end-use quality as long as the wheat is soft and white. In this case, continued breeding with a bulk population may be the best route.

If high end-use quality and high yield potential are vital to the farmer's success, the farmer and breeder can select single plants out of the bulk population and begin cultivar trials (Option B, Fig. 1). These advanced lines should have at least four seasons of trials under constant selection pressure in the target environment. Instead of choosing the best line and growing it out as a cultivar, the best 2–10 lines could be chosen, mixed together and grown as a blend. This would increase the genetic diversity of the population to be grown, thereby buffering against environmental fluctuations. Option B is less economical and more time consuming than Option A, and should only be used if a high end-use quality and/or a high yield cannot readily be realized by the existing population. In general, careful initial evaluation and choice of parental germplasm will eliminate the additional expense of utilizing the cultivar trials shown in Option B.

The bulk population should continue to be grown in a field in the target environment as a dynamic landrace capable of adapting to climatic, cultural and agronomic change. The farmer should continue to eliminate inferior or unwanted phenotypes from this landrace, as well as continuing to select out superior phenotypes for cultivar trials. The more years the bulk population is grown, the better adapted the population will become. If there is a 3-year drought, for example, superior plants chosen from this population will have genotypes and multiallelic associations that thrive under drought conditions, and these lines could then be added to the blend to increase buffering potential in future years of drought. The bulk populations developed through the EPB process are, in essence, modern landraces—heterogeneous crop varieties developed by plant breeders combined with continual farmer improvement.

Most farmers rotate crops from field to field. In many instances, the environmental variation (V_E) between these fields is high. Components of agricultural environments include spatial or location variables (temporally stable or repeatable variables, including soil characteristics and latitude), temporal variables (temporally unstable or non-repeatable variables, including seasonal or annual variation in rainfall, temperature, wind, pests and pathogens), and management variables (including fertilizer type, rotations, cover crops and irrigation)[40]. To minimize the V_E between different fields and increase heritability of selection criteria in the bulk population, a stratified bulk selection technique is appropriate (Fig. 2). Selection for traits with low heritability (e.g., yield) is more successful if V_E is minimized as much as possible. This would include the temporally stable variables mentioned above. Figure 2 represents a potential 4-year rotation on four different fields in the same farming system. If Option A of the EPB method were chosen, then only the bulk population would need to be grown in each field in order to maximize response to natural selection and management variables in each individual field. If Option B were chosen, cultivar trials in each field would produce the

best results. As the cultivar trials rotate with the target crop, it will be important to record which cultivar performed best in which field.

Implications for Low-Input and Organic Crop Breeding

Seed-supply systems have become increasingly estranged from farmers, and modern plant breeders, with corporate ties involving patents that force farmers to buy new seed from companies each year, tend to support this separation[41]. In addition, in some countries, farmers are limited in their choice of cultivar to those few varieties mandated by their government[42]. Farmers are often unable to afford these new varieties and the chemicals and fertilizers that accompany them, or may be unwilling to pattern their farming systems to suit the high-input systems under which these varieties were selected. As plant breeders put less emphasis on small-scale, low-input and/or organic farms, a plant-breeding method designed to return these farmers to the forefront of the breeding process is needed.

An evolutionary participatory breeding method is uniquely suited to improving inbred small grain crop species on a large number of low-input and organic farms. Farmer knowledge and expertise are utilized to improve crop varieties specifically adapted to their individual farming systems and local soil and climatic conditions. The EPB method emphasizes farmer participation in the breeding process, instead of farmer selection of homogeneous varieties bred under a different farming system and different environmental conditions. If low-input and organic farmers have access to bulk populations in early generations and a relatively simple, quick and inexpensive breeding method, they should be able to breed crop varieties and landraces that will help improve the sustainability and profitability of their farm. The EPB method unites plant breeders and farmers in the development of high-quality, genetically diverse, modern landraces.

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Evaluation of perennial herbaceous legumes with different phosphorus sources and levels in a Brazilian Ultisol

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Abstract

This study was carried out under field conditions with the aim of evaluating the period of time necessary for soil cover, dry matter production and accumulation of nutrients by perennial herbaceous legumes with different phosphorus sources at different levels. Four legumes were evaluated: calopo (*Calopogonium mucunoides* Desv.), forage groundnut (*Arachis pintoi* Krap. & Greg.), siratro (*Macroptilium atropurpureum* (OC.) Urb.) and tropical kudzu (*Pueraria phaseoloides* (Roxb.) Benth.). Each of these species received different phosphorus (P) sources and levels: no phosphate fertilization; 44 and 88 kg of P ha^{-1} applied as rock phosphate; and 44 kg of P ha^{-1} as triple superphosphate. Calopo, siratro and tropical kudzu completely covered the soil surface 129 days before forage groundnut. Phosphate fertilization did not increase the dry matter production of any species. The legumes forage groundnut, siratro and tropical kudzu showed desirable characteristics that promote their use as cover crops, such as high dry matter production and shoot accumulation of nitrogen (N) and potassium (K). Forage groundnut had the highest proportion of N derived from the atmosphere at the end of the rainy season, while there were no significant differences between the legumes at the end of the dry season. There was an elevation of soil pH and calcium + magnesium (Ca + Mg) contents, associated with a reduction of aluminum (Al) content, in the surface soil layer (0–5 cm) for siratro in relation to groundnut and tropical kudzu. Tropical kudzu promoted higher soil organic C contents when compared to groundnut.

Key words: biological nitrogen fixation, cover crops, phosphate fertilization

Introduction

The use of cover crops is indicated as a strategy to improve sustainability of agroecosystems, bringing benefits to both soil and crops[1]. Gliessman[2] affirmed that some cover crops may cause favorable impacts on soil structure, soil fertility and pest control, reducing the use of external inputs in agriculture. On the other hand, problems such as the increase of certain pests, like nematodes, have also been related to some cover crops[3,4]. Some characteristics are desirable for cover crops used in tree-based systems, such as improvement of crop yields; reduction of soil erosion; increase of soil organic matter, supply of nitrogen and retention of other nutrients in the soil; inhibition of weeds and suppression of pest organisms[2]. Among the plant species employed, perennial herbaceous legumes intercropped with fruit trees present great potential for improving plant production in orchards[5,6].

Perennial herbaceous legumes, which fix atmospheric nitrogen biologically, represent a strategy to recuperate degraded lands of farmers who cannot afford N fertilizers[7]. Another advantage to soil fertility brought by these plants is related to recycling of nutrients that have been leached to deep soil layers[1]. These nutrients may be absorbed by legume roots, becoming available to cultivated plants after cutting of the cover crops.

Soil covered by perennial herbaceous legumes is generally more protected against erosion[8]. This is due to the mechanical protection promoted by these cover crops, which reduces the direct impact of rain drops on the soil surface. Besides reducing erosion, perennial herbaceous legumes may also increase water infiltration in the soil[9].

Weeds cause negative effects on agriculture in many tropical areas, reducing yields. Cover crops may also allow weed control by competing for light[2], water and nutrient resources[10] or by allelopathic processes[11]. However,

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studies also indicate that some perennial herbaceous legumes may compete for water and nutrients with fruit crops, suppressing their yields[12].

Besides intercropping with fruit trees, perennial herbaceous legumes have also been used successfully as forage plants[13,14]. According to this information, plants cultivated as cover crops can also be managed by removing residues for animal feeding. It is important to understand the effects of this type of residue management on soil fertility.

In spite of the described advantages, using inappropriate species for certain soil and climatic conditions may compromise the efficiency of cover crops. Problems such as plant sensitivity to soils with low fertility are described by several authors[15]. Therefore, selecting legumes adapted to soils of low fertility is important in many tropical areas. It is equally important to consider the compatibility of the species within diverse production systems.

The process of biological nitrogen fixation requires high quantities of phosphorus (P)[16]. Consequently, phosphate fertilization represents a strategy to favor legume growth and nitrogen accumulation if the soil is P limited.

The purpose of this study was to characterize the speed with which four different perennial legumes covered the soil, their dry matter production and accumulation of nutrients in the shoot tissue, when fertilized with different phosphorus sources and at different levels. Their N fixation potential and effects on soil fertility were also evaluated, as well as the impacts of different types of residue management.

Materials and Methods

The trial was conducted on an Ultisol located at the Embrapa Agrobiologia Experimental Station, in Seropédica, Rio de Janeiro state, Brazil (longitude 43°41′W, latitude 22°45′S, 33 m above sea level). Soil chemical properties (0–20 cm depth) were analyzed following Embrapa methodology[17], showing pH (H_2O) = 5.6, exchangeable aluminum (Al; titration against NaOH) = 0.0 $cmol^{(+)}\ dm^{-3}$, exchangeable calcium (Ca; titration against EDTA) = 3.0 $cmol^{(+)}\ dm^{-3}$, exchangeable magnesium (Mg; titration against EDTA) = 1.4 $cmol^{(+)}\ dm^{-3}$, available phosphorus (P; Mehlich 1) = 2.0 $mg\ dm^{-3}$, exchangeable potassium (K) = 72 $mg\ dm^{-3}$. The annual means of temperature and rainfall were 24.1°C and 1620 mm, respectively. The dry season occurs from April to September.

A randomized complete block design was used, with three replicates, in a factorial scheme 4 × 4 (4 legumes and 4 phosphorus sources and levels), in a split-plot experiment. The main plots received legumes [calopo (*Calopogonium mucunoides* Desv.), forage groundnut (*Arachis pintoi* Krap. & Greg.), siratro (*Macroptilium atropurpureum* (OC.) Urb.) and tropical kudzu (*Pueraria phaseoloides* (Roxb.) Benth.)], and treatments with different phosphorus sources and levels (no phosphate fertilization, 44 and 88 kg of P ha^{-1} applied as rock phosphate, and 44 kg of P ha^{-1} as triple superphosphate). The subplots received two different types of residue management after legumes harvest: the legumes were harvested and the plant material left on the soil, or the plant parts were removed from the plots to simulate situations where the legume was harvested periodically as a fodder crop. According to the type of plant growth, siratro and tropical kudzu are prostrate, with a tendency to climb, while forage groundnut is a creeper plant.

The legumes were planted in February of 1995. Groundnut established poorly and had to be replanted at 75 days after trial installation. The speed at which the soil was covered was evaluated by a photographic method, using the software SIARCS[18].

Calopo, siratro and tropical kudzu were harvested at 5 and 9 months after planting. As forage groundnut was replanted in the dry season, it grew slowly, being cut for the first time at 7 months after trial installation. Calopo had problems after the first harvest, due to mite attack. The remaining species continued to be cut at 12, 21, 24, 35 and 38 months after trial installation. In all, six cuts of groundnut and seven cuts of siratro and tropical kudzu were made.

At each cut, shoot samples were collected to determine dry matter production and N, P and K contents. These samples were oven dried at 65°C until they showed constant weight. For N analysis the procedure of Bremner and Mulvaney[19] was followed, while P and K were determined after nitric-perchloric digestion[20]. P was analyzed colorimetrically, and K by flame photometry[17].

At 24 months after planting, at the end of the rainy season, shoot samples of the legumes that received triple superphosphate were also collected, with the aim of evaluating biological nitrogen fixation (BNF) by the ^{15}N natural abundance method[21]. At the same time, microplots (2.0 × 1.0 m) were demarcated in the subplots fertilized with triple superphosphate, and plant residues were removed. These microplots received 10 kg of N ha^{-1} as ammonium sulfate with 10 atom % ^{15}N, to evaluate BNF by the ^{15}N isotope dilution method[22]. As non-fixing control plants, the grasses *Panicum maximum* Jacq. ecotype KK 16 and *Brachiaria arrecta* (Hack ex T. Durand & Schinz) Stent were used. Legume and grass shoot samples were collected 35 months after planting, at the end of the dry season. The shoot samples were oven dried at 65°C, weighed and analyzed for total N and ^{15}N by mass spectrometry.

Soil samples were collected at 16 and 30 months after planting, from depths of 0–5, 5–10 and 10–20 cm, to evaluate the effect of cover crops on the following soil fertility parameters[17]: pH in water, exchangeable Al, exchangeable Ca, exchangeable Mg, available P, and exchangeable K.

Data for all variables were subjected to ANOVA procedures. Where significant differences were detected, Tukey's test was applied, at 0.05 probability level, to separate means.

Table 1. Percentage of soil covered by perennial herbaceous legumes in different periods of time.[1]

Legumes	Planting date	Percentage of soil covered at different times after trial installation							
		39 days	67 days	106 days	135 days	168 days	198 days	230 days	264 days
		(%)							
Forage groundnut	May 1995	NE[2]	NE	3	9	19	52	89	97
Calopo	February 1995	16ab	80a	93b	100a	100a	100a	100a	100a
Siratro	February 1995	22a	81a	94ab	100a	100a	100a	100a	100a
Tropical kudzu	February 1995	11c	52b	97a	100a	100a	100a	100a	100a

[1] Values in the same column followed by different letters indicate significant differences ($P \leq 0.05$) according to Tukey's test.
[2] NE, not evaluated.

Table 2. Dry matter production by perennial herbaceous legumes under two types of residue management over a period of 4 years.[1]

Legumes	Dry matter production	
	Residues left on the cultivated area	Residues removed from the cultivated area
	($Mg\ ha^{-1}$)	
1st year		
Calopo	5.6Ca	5.6Ca
Forage groundnut	13.1Ba	12.6Ba
Siratro	12.3Ba	12.7Ba
Tropical kudzu	15.2Aa	15.3Aa
2nd year		
Forage groundnut	15.0Aa	11.7Ab
Siratro	6.1Ca	6.2Ca
Tropical kudzu	9.4Ba	8.3Ba
3rd year		
Forage groundnut	5.5Aa	4.1Ab
Siratro	3.7Ba	3.5ABa
Tropical kudzu	3.4Ba	2.8Ba
4th year		
Forage groundnut	6.0Aa	4.0Ab
Siratro	4.0Ba	4.0Aa
Tropical kudzu	4.0Ba	3.4Aa

[1] Values followed by different capital letters (in the same column) or by small letters (in the same line), for each year, indicate significant differences ($P \leq 0.05$) according to Tukey's test.

Results and Discussion

Periods of time necessary for complete soil cover by the legumes varied from 135 days after planting of calopo, tropical kudzu and siratro, to 200 days after the replanting of forage groundnut (Table 1). Although after the first 135 days the first three legumes completely covered the soil surface, calopo and siratro covered the soil earlier, and at 67 days after planting showed 27 and 29% greater cover, respectively, than tropical kudzu. Groundnut was not compared to other legumes because it was replanted during the dry season, showing slower growth. Planting time influences soil cover velocity of groundnut. According to Espindola et al.[23], planting delayed from March to May, in the southeast of Brazil, caused an increase in the time necessary for complete soil cover from 130 to 190 days.

The periods of time for complete soil cover by the evaluated legumes were considerably larger than those values described for the annual legume velvet bean (*Mucuna pruriens*) on the same soil and climate conditions[23], emphasizing the importance of controlling weeds during the first months after planting for the perennial legumes.

Higher values were observed for dry matter production (Table 2) and accumulation of N, P and K (Table 3) in tropical kudzu during the first year compared to the other legumes. Forage groundnut overtook other legumes in dry matter production and accumulation of N during the following years. Considering the results during the first year, tropical kudzu produced up to 72% more dry matter than the other legumes, and it was superior to other species by up to 115, 88 and 262% for accumulation of N, P and K, respectively. The results described above were probably influenced by the fact that groundnut was replanted at 75 days after trial installation, having less time to produce dry matter and accumulate nutrients than the other species during the first year.

It is important to point out that high values observed in the first year for dry matter production and nutrients accumulation, compared to the second year, are related to the greater number of cuts made during that period (three in the first year against two in each of the next years).

From the second year onwards, prejudicial effects of removing plant residues were detected on dry matter production (Table 2) and nutrient accumulation (Table 3). There were different results between the evaluated legumes, with only forage groundnut being affected by residue management. Considering nutrient recycling, the two types of residue management have different effects on the sustainability of agroecosystems, with removal after the cut contributing to a higher exportation of nutrients. Natural leaf fall was observed in tropical kudzu and siratro in both the harvested and unharvested plots, which would reduce the effect of residue removal on soil nutrient supply. Consequently, residue removal of forage groundnut for agricultural practices such as hay production would only be viable if limiting soil nutrients are replaced by fertilization.

Table 3. Nitrogen, phosphorus and potassium accumulation by perennial herbaceous legumes under two types of residue management over a period of 4 years.[1]

Legumes	N accumulation		P accumulation		K accumulation	
	Retained[2]	Removed[3]	Retained[2]	Removed[3]	Retained[2]	Removed[3]
	(kg ha^{-1})					
1st year						
Calopo	139.7Ca	139.7Ca	11.4Da	11.4Da	45.0Da	45.0Da
Forage groundnut	354.9Ba	341.4Ba	22.5Ca	21.9Ca	93.7Ca	87.4Ca
Siratro	358.7Ba	349.4Ba	26.7Ba	26.7Ba	141.6Ba	128.4Ba
Tropical kudzu	438.9Aa	421.4Aa	32.8Aa	30.6Aa	208.1Aa	170.9Aa
2nd year						
Forage groundnut	406.0Aa	320.0Ab	27.1Aa	20.0Ab	92.2Aa	63.7Ab
Siratro	187.0Ca	178.6Ba	12.2Ba	11.9Ba	57.2Ba	58.5Aa
Tropical kudzu	270.6Ba	233.1Ba	17.4Ba	16.1ABa	79.8ABa	66.2Aa
3rd year						
Forage groundnut	179.7Aa	129.8Ab	10.4Aa	7.3Ab	42.3Aa	23.5Ab
Siratro	109.6Ba	102.9Ba	6.0Ba	5.6Aa	32.3Aa	28.6Aa
Tropical kudzu	98.2Ba	77.9Ca	5.9Ba	4.8Aa	25.6Aa	18.9Aa
4th year						
Forage groundnut	181.5Aa	123.5Ab	12.9Aa	10.4Ab	52.8Aa	23.5Ab
Siratro	121.5Ba	115.8Aa	9.0Ba	8.5ABb	52.7Aa	48.5Aa
Tropical kudzu	129.0Ba	102.7Aa	9.0Ba	7.2Bb	44.9Aa	30.8Aa

[1] Values followed by different capital letters (in a column) or by small letters (between 'Retained' and 'Removed' within each species), for each year, indicate significant differences ($P \leq 0.05$) according to Tukey's test.
[2] Retained = residues left on the cultivated area.
[3] Removed = residues removed from the cultivated area.

Table 4. Delta ^{15}N values ($\delta^{15}N$), proportion of N derived from biological nitrogen fixation (BNF; % Ndfa), and amounts of N fixed by perennial herbaceous legumes, estimated using the natural abundance of ^{15}N method with two different non-fixing control plants, at the end of the rainy season (24 months after planting). The legumes had been fertilized with phosphorus (44 kg ha^{-1} as triple superphosphate).[1]

Legumes/control plants	$\delta^{15}N$	% Ndfa		Amounts of N fixed	
		P. maximum	*B. arrecta*	*P. maximum*	*B. arrecta*
		(%)		(kg ha^{-1})	
Forage groundnut	0.40c	90.8a	88.6a	159.9a	158.0a
Siratro	1.69a	68.7c	59.8c	70.5a	61.9a
Tropical kudzu	0.88b	84.2b	78.5b	107.9a	100.2a
Control plants					
P. maximum	5.12	–	–	–	–
B. arrecta	4.18	–	–	–	–

[1] Values in the same column followed by different letters indicate significant differences ($P \leq 0.05$) according to Tukey's test.

Considering all the cuts made of forage groundnut, tropical kudzu and siratro, it is significant to note their high potential for dry matter production and shoot accumulation of N and K. Forage groundnut produced 36 Mg of dry matter ha^{-1} and accumulated 1018 kg of N and 240 kg of K ha^{-1}, while tropical kudzu and siratro produced 31 and 26 Mg of dry matter ha^{-1}, respectively, and accumulated 886 and 762 kg of N ha^{-1}, and 323 and 274 kg of K ha^{-1}, respectively.

There were no significant differences between types of residue management for biological nitrogen fixation (BNF), evaluated using the ^{15}N natural abundance method obtained at the end of rainy season (Table 4). The results showed higher proportion (88.6–90.8%) of N fixed for forage groundnut, which was superior to other species by up to 28%. All the legumes presented high amounts of N fixed per hectare, varying from 62 to 160 kg of N ha^{-1}. Since P is supposed to increase N fixation, the obtained results should be observed with caution, because they were measured only in the plots fertilized with triple superphosphate, and therefore do not represent BNF of legumes without fertilization.

Table 5. Atom % ^{15}N atoms in excess, proportion of N derived from biological nitrogen fixation (BNF; % Ndfa) and amounts of N fixed by perennial herbaceous legumes estimated using the ^{15}N isotope dilution method, with *Brachiaria arrecta* as the non-fixing control plant, at the end of the dry season (35 months after planting). The legumes had been fertilized with phosphorus (44 kg ha^{-1} as triple superphosphate).[1]

Legumes/control plant	^{15}N atoms in excess	% Ndfa	Amounts of N fixed
	(%)		(kg ha^{-1})
Forage groundnut	0.045a	67.5a	100.4a
Siratro	0.018a	86.8a	100.6a
Tropical kudzu	0.047a	66.6a	49.3a
Control plant			
B. arrecta	0.139	–	–

[1] Values in the same column followed by different letters indicate significant differences ($P \leq 0.05$) according to Tukey's test.

Table 6. Chemical properties [(a) pH, exchangeable Al, Ca+Mg; and (b) organic C, available P and K] of the soil covered by perennial herbaceous legumes, at three different depths (0–5, 5–10 and 10–20 cm).[1]

(a)

	Perennial herbaceous legumes								
	Forage groundnut			Siratro			Tropical kudzu		
Depth (cm)	pH	Al	Ca+Mg	pH	Al	Ca+Mg	pH	Al	Ca+Mg
		(cmol$^{(+)}$ dm^{-3})			(cmol$^{(+)}$ dm^{-3})			(cmol$^{(+)}$ dm^{-3})	
0–5	4.5Ab	0.13Cb	4.2Ab	5.0Aa	0.01Bc	4.7Aa	4.5Ab	0.15Ba	4.1Ab
5–10	4.3Ba	0.20Aa	3.5Bb	4.5Ba	0.16Ab	3.9Ba	4.5Aa	0.16Ab	3.8Ba
10–20	4.5Aa	0.15Bb	3.5Ba	4.5Ba	0.16Aa	3.6Ca	4.5Aa	0.14Cc	3.6Bb

(b)

	Perennial herbaceous legumes								
	Forage groundnut			Siratro			Tropical kudzu		
Depth (cm)	Organic C	P	K	Organic C	P	K	Organic C	P	K
	(g kg^{-1})	(mg dm^{-3})		(g kg^{-1})	(mg dm^{-3})		(g kg^{-1})	(mg dm^{-3})	
0–5	7.0Ab	5.8Aa	53.0Aa	7.7Aab	4.9Aa	57.0Aa	8.1Aa	5.6Aa	59.0Aa
5–10	6.9Bb	4.5Ba	28.0Ba	7.1Bab	4.1Ba	27.0Ba	7.2Ba	4.4Ba	40.0Ba
10–20	5.1Cb	4.0Ca	21.0Ba	5.3Cab	3.9Ca	25.0Ba	6.0Ca	3.9Ca	30.0Ba

[1] Values followed by different capital letters (in a column) or by small letters (between species for each soil parameter) indicate significant differences ($P \leq 0.05$) according to Tukey's test.

Using the enriched ^{15}N isotope dilution method, at the end of dry season, there were no significant differences between legumes for proportions or amounts of N fixed per hectare when *Brachiaria arrecta* was used as the non-fixing control (Table 5). Negative results were obtained with the use of *Panicum maximum* ecotype KK 16, suggesting that this species is not a good reference plant for use with the legumes evaluated by the ^{15}N isotope dilution method (data not shown). This may be related to differences in rooting patterns or in N uptake between the nitrogen-fixing plant and the non-fixing reference plant[24]. Comparing the ^{15}N natural abundance method with the ^{15}N isotope dilution method, Giller and Wilson[24] observed that, as the variation in $\delta^{15}N$ of available soil N with depth is usually small, the closeness with which the rooting patterns of the legumes and non-fixing controls need to be matched is not as critical in the ^{15}N natural abundance method as when using ^{15}N isotope dilution.

The results presented for nitrogen fixation in the plots where P was added to the soil are consistent with other reports[7,24], indicating the potential of the legumes evaluated in this study for adding large amounts of nitrogen to agroecosystems. However, some agricultural practices may affect the benefits of BNF. Successive cuts of perennial herbaceous legumes followed by removing plant residues temporarily reduce nitrogen fixation, due to the competition for carbohydrates between plant regrowth and nodule maintenance[25]. On the other hand, intercropping with

non-legume plants reduces the prejudicial effects of cutting perennial legumes on nitrogen fixation, since those species act as a sink of N fixed[24].

The different levels of phosphate fertilization did not increase dry matter production of any legume (data not shown), demonstrating that the evaluated species are adapted to soils with low P fertility. Forage groundnut is indicated in the literature as a species capable of exploiting available P of the soil, even at high aluminum contents[26]. The tolerance of herbaceous legumes to soils with low available P is related to processes such as symbiosis with arbuscular mycorrhizal fungi[27] and secretion of phytase from plant roots[28], among other mechanisms.

Soil fertility evaluation, 16 months after planting, revealed significant interactions between legumes and soil depths for pH values, and exchangeable Al and Ca+Mg contents (Table 6a). Siratro presented higher pH values and Ca+Mg contents, associated with lower Al contents, in the 0–5 cm layer, when compared to forage groundnut and tropical kudzu.

Tropical kudzu promoted an accumulation of organic C in the soil statistically higher to forage groundnut at all the evaluated layers (Table 6b). A similar effect of tropical kudzu on soil organic matter has been reported[29], corroborating the benefit of this species to soil fertility.

Regarding plant residue management, an increase of exchangeable Ca+Mg and K contents was observed in the surface layer of the soil (0–5 cm) in the subplots where residues were cut and left on soil surface, contrasting with subplots where residues were cut and removed (data not shown). Consequently, residue management may also affect soil fertility, improving soil nutrient contents in the areas where residues are left on soil surface.

Results related to the second soil fertility evaluation, made at 30 months after planting, were similar to those formerly presented, and the data are not shown here.

Further understanding of the interactions between the evaluated perennial herbaceous legumes and fruit trees, involving aspects such as yield, mineral nutrition, pests, tolerance to shade and plant management, is required to ensure that appropriate cover crops are recommended for use in orchards.

Conclusions

Calopo, tropical kudzu and siratro covered the soil surface faster than other legumes, indicating that these species may contribute to protect soil against erosion and reduce the necessity of controlling weeds after planting.

Forage groundnut, tropical kudzu and siratro demonstrated high potential for dry matter production and shoot accumulation of N and K, being superior in this respect when compared to calopo, which suffered from mite attack. Such problems may limit the use of this cover crop in orchards.

In relation to biological nitrogen fixation, special attention should be given to forage groundnut, which showed a higher proportion of N fixed at the end of the rainy season, with P application. This characteristic allows reduced nitrogen fertilizer use in orchards. Different levels of phosphate fertilization did not increase dry matter production for any legume, indicating that the evaluated species are adapted to soils of low fertility. Besides, legume cultivation had an impact on soil chemical properties. Siratro increased soil pH and Ca+Mg contents, and reduced Al contents in the surface layer of the soil (0–5 cm) when compared to groundnut and tropical kudzu. Tropical kudzu promoted higher soil organic C contents when compared to groundnut. The results obtained suggest that both legumes improve soil fertility in orchard production systems.

According to this study, the use of forage groundnut, tropical kudzu and siratro as cover crops, with residues retained in the cultivated area, is an agronomic practice that furnishes high quantities of organic material and nitrogen to the soil and contributes towards sustainability in orchards.

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Book Review

Agriculture as a Mimic of Natural Ecosystems. Edited by E.C. Lefroy, R.J. Hobbs, M.H. O'Connor, and J.S. Pate. 1999. Kluwer Academic Publishers, Dordrecht. 492 p. US$210.00, ISBN 0–7923–5965–8, hardbound.

Acknowledgement of the severe and varied negative environmental consequences of contemporary commercial agriculture is widespread. However, no similarly broad consensus on appropriate strategies for increasing agricultural sustainability has yet been reached. One such strategy, appealing in its more integrated approach to problems of agriculture, is the redesign of farming systems as structural and functional mimics of the natural ecosystems they have replaced. *Agriculture as a Mimic of Natural Ecosystems* offers a deep assessment of the validity of the mimic concept, from its fundamental underpinnings in ecological and systems theory through pragmatic operational concerns of implementation.

The book consists of the proceedings of a workshop of the same title held near Perth, Australia, in 1997. The first of the book's five sections contains two chapters authored by Wes Jackson, in recognition of his role as the inspiration for the workshop. These set the context and identify the issues addressed in the remainder of the book. The first (Jackson and Jackson, Chapter 2) describes the first two decades of research by Jackson and others at the Land Institute in Kansas, while the second (Jackson, Chapter 3) provides the historical and ecological context that motivates the work. The focus is on the development of perennial grain polycultures as functional mimics of the native prairie ecosystems of central North America. Following the designation of four functional groups present in the native community (warm- and cool-season perennial grasses, perennial legumes and perennial sunflowers), candidate species in each group were identified for potential incorporation in an artificial agricultural mimic system. Experiments with those candidate species have focused on evaluating the sustainability of perennial grain polycultures by testing whether they: (1) exhibit trade-offs between perenniality and yield; (2) outyield the same species in monoculture; (3) maintain fertility with low to no external inputs; and (4) control pests and pathogens.

The second section's three chapters address each of these questions in a broad treatment of the conceptual issues involved in agricultural mimicry of natural ecosystems. Ewel (Chapter 4) identifies four climatic zones based on their compatibility with agriculture, focusing on a suitable zone in the humid tropics. There, low abiotic stress combined with high biotic 'intricacy' favors agricultural systems that incorporate existing diversity rather than simplifying it. Ewel identifies appropriate goals for functional mimics of such systems as: (1) channeling the existing high productivity into nutritionally and economically valuable species; (2) employing those species' perenniality to maintain fertility, limit erosion, and maximize resource capture; and (3) balancing levels of diversity between ease of management and stability. Main (Chapter 5) follows that final point with an insightful essay on determining the appropriate level of diversity. Emphasizing the dynamism of all systems, he concludes that that level, as well as the relevant diversity components (i.e. genetic, species and ecosystem), is ultimately determined by the specific functionality desired. Closing the second section, Hobbs and Morton (Chapter 6) touch on the same question in a consideration of the historical development of ecology as a discipline and its role in the design of sustainable agricultural systems. Of the criteria listed by Jackson and Jackson (Chapter 2), the chapters in this section do not directly address the issue of trade-offs. They concur in their conclusions that perennial polycultures can have greater yields, maintain fertility, and control pests to a greater degree than their constituent species grown in monoculture. However, both Ewel (Chapter 4) and Main (Chapter 5) echo the concern that increased diversity may sometimes *increase* susceptibility to pests, as in the case of cassava, which in some studies was attacked even more heavily by leaf cutter ants when grown in a mixture of crops than in monoculture. Diversity, then, is a more effective barrier to pests when species identity is considered along with aggregate richness in planning its deployment.

The third section is composed of six profiles of perennial polycultures from various locations around the world. In the first of these, Joffre et al. (Chapter 7) deliver a comprehensive analysis of the dehesa savannas of southwestern Spain. Drawing on paleoecological and archeological data, they present evidence that the convergence of constraints due to water availability, nutrient limitation, and human management has given rise to the current system via a lengthy process of more or less unconscious mimicry of the natural system.

Trenbath (Chapter 8) addresses the criteria formulated by Jackson and Jackson (Chapter 2) in an assessment of various multicrop farming systems from India (as well as Thailand and the Philippines). Focusing on bicultures of herbaceous legumes and grains, he translates increased multispecies yields into reductions in the area needed to feed a farm family, thus maximizing the remaining area available for production of commercial crops on small

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farms. Subsequent portions of this chapter discuss the question of appropriate levels of agricultural species diversity, for criteria of stability (measured as constancy of overall production from year to year), resilience (ability of systems to recover from disturbance), and ecological sustainability (in terms of both soil fertility and human carrying capacity). All of these measures are increased in the multispecies case relative to monoculture, but with the consequence of increased management complexity.

Ong and Leakey (Chapter 9) and van Noordwijk and Ong (Chapter 10) focus on tree–grass interactions in savanna systems in Africa and India. The first chapter attempts to explain the different behaviors of natural savannas, in which productivity of the herbaceous layer under trees increases as precipitation declines, and agroforestry, in which the pattern is the opposite. As in the description of dehesas by Joffre et al. (Chapter 7), the authors equate the discrepancy to a difference in successional stage. Savanna trees are typically mature, with a large canopy creating greater water savings through shading and reduced evaporation than the amount transpired by the relatively small canopy leaf area. Agroforestry, with its preference for rapid-growing trees that quickly attain harvest size, represents an earlier successional stage, with tree canopy transpiration increasing more than soil evaporation declines. The following chapter applies these concepts to an assessment of the suitability of savanna mimics on African farms. In general, increased productivity and/or complementarity of resource use occur only when the woody component consists of old trees spared during field clearing, rather than newly planted ones. Offering another perspective on appropriate levels of diversity, the authors identify, in agreement with Trenbath (Chapter 8), the potential of a mixture of species adapted to different annual rainfall patterns for stabilizing overall production.

In the penultimate contribution to the section, Neher (Chapter 11) considers belowground diversity in natural and agricultural ecosystems, reviewing the importance of soil organisms in ecosystem function and the changes in their composition in response to agricultural intensification, and highlighting areas of future research on this important component of agricultural mimicry. Presaging the following section, Stirzaker (Chapter 12) examines the problems of excess deep drainage in irrigated horticultural systems, and the potential for their amelioration via intercropping with deep-rooted lucerne.

The volume's fourth section delivers a detailed analysis of the problems of conventional agriculture in southern Australia, and the potential of agricultural mimics to ameliorate them. As summarized by Hatton and Nulsen (Chapter 13), native woodland and savanna ecosystems, with deep roots and continuous high leaf area, either evaporate or transpire nearly all annual precipitation. Replacement of these systems with conventional annual crop and pasture systems permits deep drainage, raising the water table and bringing salts into the crops' root zone. Grierson and Adams (Chapter 14) add that conventional agriculture reduces the complementarity in both space and time of plant P and N use. Pate and Dawson (Chapter 15) provide a detailed ecophysiological analysis of these disruptions to native-system nutrient cycles using stable-isotopic techniques, and offer insights as to how those methods can contribute to the evaluation of potential mimics. Lefroy and Stirzaker (Chapter 16) assess the potential of agroforestry systems to restore rising water tables to their previous levels, comparing the segregation, integration, and rotation of trees with crops. Dunin et al. (Chapter 18) conduct a similar assessment with lucerne rather than woody perennials. In keeping with the principle that the system to be mimicked must first be understood, Pate and Bell (Chapter 17) characterize native *Banksia* woodlands, offering a spectrum of intervention ranging from outright restoration of native communities to integration of native species with desirable functional traits in existing agricultural systems. Hobbs and O'Connor (Chapter 19) offer a similar presentation for native salmon gum (*Eucalyptus salmonophloia*) and heathland ecosystems.

The fifth and final section is concerned with the social and economic implications of agricultural mimics. Pannell (Chapter 20) makes the key observation that even the soundest ecological design will not be widely adopted without meeting key criteria in farmers' perceptions. Passioura (Chapter 21) identifies the mosaic nature of landscapes as another pattern that must be considered in the implementation of agricultural mimicry. Lefroy et al. (Chapter 22) cap off the volume with an insightful summary that extracts meaningful connections from the book's diverse set of perspectives and study systems. They emphasize the importance of identifying the attributes of natural systems that are of interest for mimicry in agriculture, and specify that those relevant for sustainability include increased diversity for its functional relation to 'persistence, resilience, and efficiency of resource capture', based on the recognition of individual species' adaptations to a given setting.

Trade-offs appear at many different levels in the various contributions—whether as perennating versus reproductive investment in individual plants (Jackson and Jackson), reduction in deep drainage versus reduced productivity in tree–grass interactions (various), or high yield versus sustained fertility and stability versus management complexity (Trenbath). These are almost uniformly discouraging, particularly in the Australian example. However, Lefroy et al. (Chapter 22) highlight the case of Tasmanian blue gum (*Eucalyptus globulus*) as an instance in which adaptive management has maintained production and farmer income while restoring desirable functional attributes of native ecosystems, and on a shorter timeline than that often envisioned for the development of agricultural mimics (e.g. Jackson and Jackson, Chapter 2; Hobbs and Morton, Chapter 6).

While acknowledging that any agricultural mimic must equal or better the current system's return to the farmer, the book's main emphasis is on agriculture in industrialized

countries, and hence on commercial crop production. Trenbath's focus on farming systems where food sufficiency is the primary goal (Chapter 8) is absent from most other contributions. Similarly, some authors opine that the role of agriculture is to feed the cities, with the implicit assumption seeming to be that the forces that gave rise to widespread monoculture are separate, and distinct in their reversibility, from those driving the ongoing global urbanization of population and concurrent consolidation of agricultural land tenure. By overlooking the syndrome of high productivity and diversity and intense management that characterizes many small farms worldwide, the volume passes over key factors that might increase both the viability and area of impact of agricultural mimicry.

Likewise, although the importance of scale is noted throughout, the volume as a whole tends to overlook higher levels of organization than the landscape, although their consequences for the development of working agricultural mimics may be as profound. While dehesas were productively maintained in their present form for centuries, recent decades have witnessed a decline in their area in favor of monoculture grainfields and forestry plantations (Joffre et al., Chapter 7). These shifts are due primarily to political shifts in agricultural policy, and may be exacerbated by global climate change. Given the multidecadal time horizons projected for the development of mimic systems, the centuries required for the development of dehesa stand as a potent reminder of the higher-level phenomena, both human and natural, that may hinder the successful design and execution of agricultural mimics independent of the systems' internal coherence and sustainability.

Each of these issues could spawn multiple volumes in and of itself, and the fact that this single book raises all of them does it much more credit than the absence of comprehensive treatment can subtract. Given its origins, it is understandable that two-fifths of the volume are devoted to southern Australia. Although this tends to yield a gloomier prognosis for the mimic concept, and precludes deeper or more wide-ranging treatment of other cases, there is undeniable value in the depth of understanding that such focus affords of the practical challenges in applying concepts of ecological mimicry to the farming systems of a particular region. Overall, the book is a valuable store of information on the current state and future prospects of ecological mimicry in agriculture. Whether readers seek an introduction to the concept, or a durable reference on the technical status of the field, this volume is a sound investment.

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